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Biological control of two-spotted spider mites using phytoseiid predators. Part I

Modelling the predator-prey interaction at the individual level

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Abstract

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The searching behaviour of individual predators of four phytoseiid species (*Phytoseiulus persimilis, Amblyseius potentillae, Amblyseius bibens, Metaseiulus occidentalis*) is investigated in relation to the two-spotted spider mite (*Tetranychus urticae*), which infests greenhouse roses. Especially the role of spider-mite webbing in the predator-prey relation is studied. Webbing interferes with searching, decreasing the rate of encounter per unit prey density. Low walking speeds and activity in webbing ensure that the predator is rarely disturbed after contact with other mites. Webbing also positively influences searching, as spider mites aggregate within the webbed area: prey density, defined here as the number of prey per square centimetre of webbed leaf area, is high, as is the rate of encounter with prey. The ability to capture a prey after tarsal contact depends on the food content of the gut, the prey-stage and, in two specific cases, the webbing; the success ratio of *P. persimilis* increased on a webbed substrate, that of *A. potentillae* decreased.

Models to simulate rate of predation on the basis of the dynamics of the motivational state and the state dependent rate of successful encounter are proposed. The food content of the gut is chosen as an indicator of the motivational state. A stochastic queueing model simulates predation as accurately as a Monte Carlo model or a compound simulation model. The queueing model is preferred because of its economic use of computer time and the relatively few variables used. The model was validated in predation experiments.

Systems analysis showed that the effect of temperature on the rate of predation is largely determined by its relation with the relative rate of food conversion into egg biomass and not by behavioural changes related to temperature. Also, it was shown that webbing has an important influence on the predation rate. A new model for the analysis of prey-stage preference is proposed.

Predators invade the webbed leaf area after contact with the silk strands, irrespective of the presence of prey. The residence time in the prey colony is determined by prey density. Simulation of experimentally defined walking behaviour shows that predators remain in profitable prey patches by turning at the edge of the webbed leaf area. However, when predator density increases, the tendency to leave the prey colony also increases, even at high prey densities. Only *A. potentillae* avoided the webbed leaf area, preferring the thickest parts of the leaf ribs or other protected places on the plant.

A survey of references on life history data is presented; emphasis is given to the role of food, temperature and relative humidity. Experiments by the author show that oviposition history of predatory females is a major factor in determining the actual rate of food conversion into egg biomass; and that the egg stage of the predators is very vulnerable to relative humidities below 70%, though the evapotranspiration of the plant and the hygroscopic properties of the webbing buffer this to some extent. As the juvenile mortality of the phytoseiids increases above 30°C, and that of the two-spotted spider mites above 35°C, spider-mite control at temperatures above 30°C is not effective.

The four phytoseiid species are ranked on their capacities for numerical increase and predation: *P. persimilis, A. bibens, M. occidentalis* and *A. potentillae*. On capacity to survive on alternative foods they are ranked: *A. potentillae, A. bibens, M. occidentalis* and *P. persimilis*. Some trials with alternative food supply did not improve survival rates established for prevailing greenhouse conditions.

The rate of increase of the webbed area per individual spider mite is quantified by experiment. This knowledge will enable continuous monitoring of the prey density during simulations of the predator-prey interactions on the population level.

Free descriptors: biological control, natural enemies, Phytoseiidae, Tetranychidae, webs, searching behaviour, prey stage preference, predation, dispersal, deterministic simulation models, stochastic simulation models, life history.

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This report will also be used as a doctoral thesis for graduation as Doctor in de Landbouwwetenschappen at the Agricultural University, Wageningen, the Netherlands.

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APPENDICES

1 Introduction

1.1 CONTROL OF SPIDER-MITE OUTBREAKS

Spider Mites (Acarina: Tetranychidae) are a continuous potential danger to many food and ornamental crops. Their high reproductive potential and rapid development form the basis for a high capacity of population increase. Hence the outbreaks can develop even shortly after pesticide treatment. Moreover, they appear to develop resistance to many chemicals that initially gave effective control (Helle & van de Vrie, 1974). This results in a vicious circle of pesticide development and resistance. Therefore alternative control strategies need to be developed. Apart from supervised control strategies there are four major alternatives:

- plant breeding for resistance to spider mites (e.g. de Ponti, 1977a).
- genetic control strategies

. to reduce the fertility of female spider mites by the introduction of sterilized males (Nelson, 1968; Nelson & Stafford, 1972) or males with chromosomal rearrangements (van Zon & Overmeer, 1972; Overmeer & van Zon, 1973).

. to displace the endemic spider-mite population by a mite strain that is not resistant to certain pesticides or very sensitive to extreme temperatures, which can be easily brought about in greenhouses (Feldmann et al., 1981).

- control by a fungal epidemic in the mite population (Shagunina, 1977; Gerson et al., 1979).
- control by predators (e.g. Huffaker et al., 1970).

The choice of a specific method or a combination of methods depends very much on agricultural practice and the demands of the grower/consumer with regard to the product. The present study aims to elucidate the potential role of some predatory mites (Acarina: Phytoseiidae) for the control of the two-spotted spider mite, *Tetranychus urticae* (Acarina: Tetranychidae), by systems analysis so that new options for integrated pest management may be developed and compared with alternative control strategies. The results of these studies are described in two subsequent Agricultural Research Reports concerning investigations in the laboratory (Part 1) and the greenhouse (Part 2).

1.2 DESCRIPTION OF THE PREDATOR-PREY SYSTEM

The two-spotted spider mite, *Tetranychus urticae* Koch, is a serious pest in the greenhouse culture of ornamental roses. Since 1967, dienochlor [perchlorobi(cyclopenta-2,4-dienyl)] has been used for chemical control of this spider mite in ornamental crops. Because pesticide resistance may evolve (McEnroe & Lakocy, 1969), alternative methods of crop protection have to be investigated. It is desirable to replace chemical spraying by biological control. Encouraged by the successful use of *Phytoseiulus persimilis* as a controlling agent of the two-spotted spider mite in greenhouse cucumbers in the 'Westland' district of the Netherlands (Bravenboer, 1963; Woets, 1976), some rose growers started to use this predatory mite with reasonable success (van de Vrie, personal communication). As in cucumbers, the predators are introduced at each spider mite outbreak.

This method of spider-mite control will only be accepted by the majority of the growers if it can be achieved with no decrease in rose production or quality and if it costs no more than treatment with chemical pesticides. Moreover, because rose bushes are exploited for 5-7 years, the use of predatory mites would be especially attractive if long-term control could be achieved with only a few initial predator introductions. These requirements can not be met as yet, so that a critical evaluation of the use of predatory mites is necessary. That evaluation should include assessment of the economic-damage level and quantification of the potential for control by the predatory mites. The economic-damage level is being studied by van de Vrie, an entomologist at the Research Station for Floriculture in Aalsmeer, The Netherlands. Studies on the potential for control by predatory mites, done upon van de Vrie's suggestion, are the topic of this report.

The substrate of *Tetranychus* consists of leaflets, shoots, bushes and hedges (Fig. 1). The rose shoots that rise above the hedges are harvested at an early stage of flowering. Because quality roses have to be free of

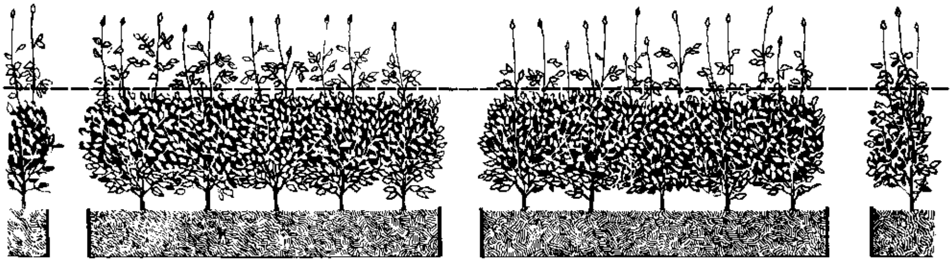


Fig. 1. Greenhouse culture of ornamental roses. Cross section of rose hedges separated by walking paths. Dotted line indicates the boundary between the 'maintenance' leaves and the leaves of the rose shoots that will be harvested.

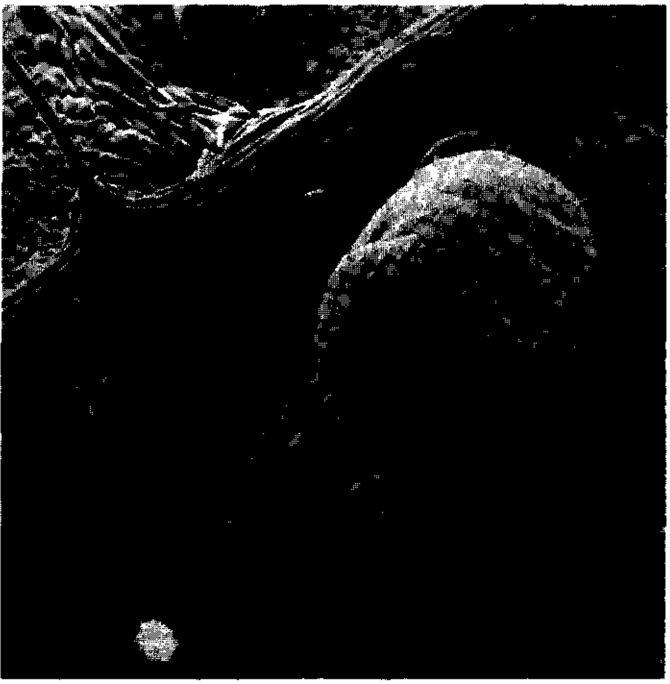


Fig. 2. Scanning electron micrograph (magnification 50 ×) of the oviposition female of *Tetranychus urticae*.

any damage, the leaves of these shoots should be carefully protected against spider-mite infestation. On the other hand, it is acceptable for the hedge beneath the economically important part to be slightly damaged.

Adult females (Fig. 2) are the founders of the spider-mite aggregations on the underside of the leaves, which are frequently located near to an edge or a rib of the leaves. The juveniles (egg, larva, protonymph, deutonymph and the different moulting stages) and the adults live in self-produced webbing. The pre-ovipositional females disperse after mating to other leaves, where they begin new colonies. The population growth and dispersal apparently result in compact foci of infestation. The upward dispersal out of the hedge leads to colonization of the upper leaves of the rose shoots. This must be prevented by one or more introductions of predatory mites.

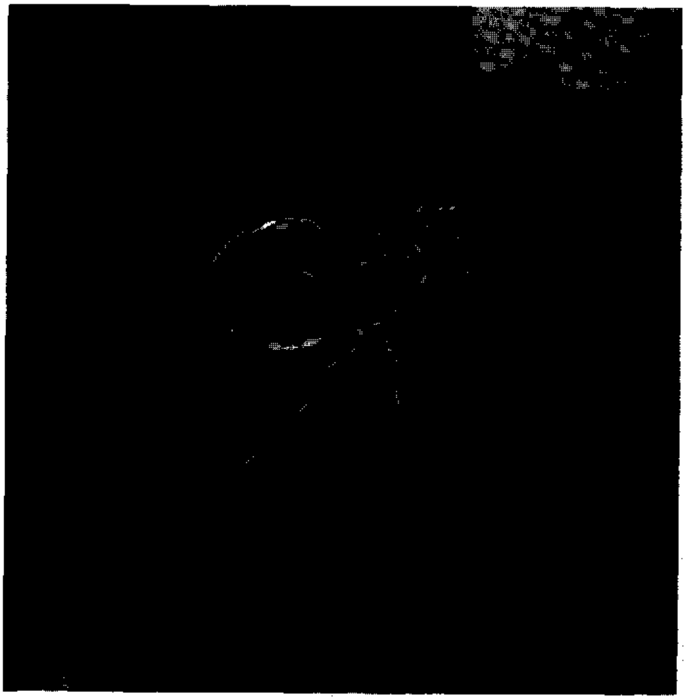
The mites feed on the leaf parenchyma, which causes spots that reduce the immaculate appearance required of quality roses. Losses caused by mite feeding are more serious therefore than in other greenhouse crops, like the cucumber or Gerbera, where the fruits or the flowers are sold and not the leaves, so that only the photosynthetic function of the leaves is of concern.

Clearly, predatory mites must prevent the upward dispersal of the plant-

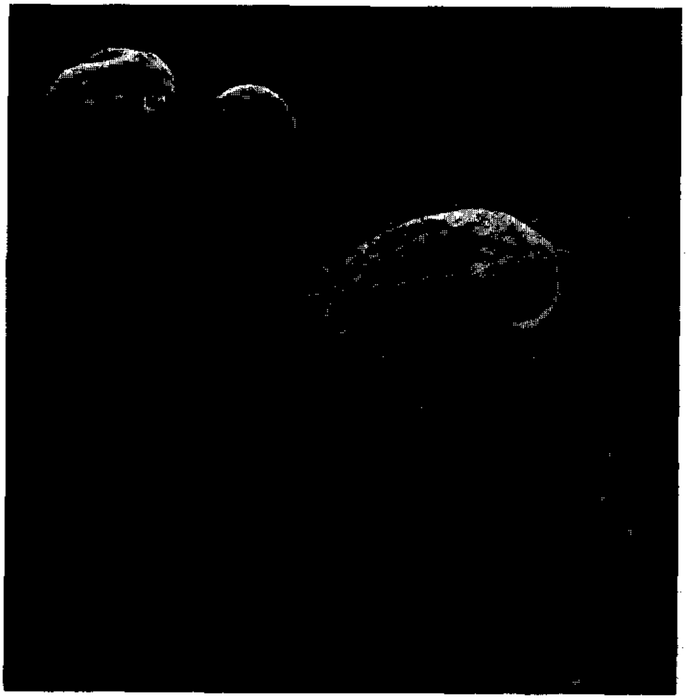
A. *Phytoseiulus persimilis.*

B. *Amblyseius potentillae.*

Fig. 3. Scanning electron micrographs (magnification 50 ×) of ovipositing females of four phytoseiid species.



C. *Amblyseius bibens.*



D. *Metaseiulus occidentalis*

feeding mites from the hedge by controlling the prey population within the hedge. Phytoseiid mites feed on all stages of the spider mite and deposit their eggs in the spider mites' webbing. The sequence of developmental stages is similar to that of the spider mites, but much less time for moulting from one stage to the other is required. Similar to spider mites, only female adult phytoseiids disperse, and only after mating. However, in contrast to their prey they do not disperse predominantly in the pre-oviposition phase, but rather during their whole adulthood. How the tetranychid and phytoseiid females disperse from colony to colony, leaflet to leaflet, shoot to shoot or hedge to hedge, and the factors that induce their dispersal are major topics of this report.

Because the time needed for the spider-mite population to double varies between only 2-4 days, their numerical increase is rather explosive. Hence the timing, the dose and the potential for control by the phytoseiid species used is of crucial importance, the more so because - in contrast to immediate extermination by acaricide spraying - the prey numbers keep increasing for some time after predator release. The increase of colonized area and the time lapse between predator release and decline in prey numbers will be treated in Part 2 of this Agricultural Research Report (to be published). These problems are investigated for four phytoseiid species: *Phytoseiulus persimilis*, *Amblyseius potentillae*, *Amblyseius bibens* and *Metaseiulus occidentalis* (Fig. 3).

Because a spider-mite outbreak cannot be easily detected in its early stages by a grower, the possibility of leaving this task to the predators was investigated. Special attention was therefore given to the ability of the predator to search for scarce prey aggregations, to withstand starvation and to survive on alternative food in periods of spider-mite scarcity. Although the four phytoseiid species studied are more or less specialized predators of tetranychids, there are conspicuous differences in their dietary range. These are treated in Part 1. The problem of choosing a favourable combination of predatory capacity and dietary range for the control of two-spotted spider mites in the greenhouse culture of ornamental roses will be treated in Part 2.

1.3 EXTRAPOLATION FROM LABORATORY TO GREENHOUSE

Experiments in which predatory mites are introduced into greenhouses to control spider mites have in some cases been successful (Huffaker et al., 1970). Observations in the greenhouse (population estimates, assessment of predator-prey ratios and distributions) and laboratory experiments (life tables, predation rates, mutual interference among predators, effects of spider-mite crowding) with several tetranychid and phytoseiid species have formed a basis for the understanding of the damaging capacity of the prey and the controlling potential of the predators. It is tempting to extrapolate laboratory observations to the practical greenhouse situation, but such extrapolations need to be validated. This problem can best be tackled by modelling the predator-prey system, computing the population fluctuations with the model and comparing the results with data gathered in the greenhouse.

Such a study may provide interesting starting points for further research in an iterative process of evaluation and design. Maybe practical results will follow, but it is not suggested that this method will give rise to fully reliable control methods by itself; large-scale validation under different conditions generally takes an excessive amount of time and models cannot approach the complexity of biological systems, if only because of the limited capacity of computers. Nevertheless attempts to validate concepts of biological systems need encouragement as they lead to a better insight into the use of biological control agents in an agro-ecosystem. Examples of such validations can be found in the modelling studies of Fransz (1974: *Tetranychus urticae - Metaseiulus occidentalis*), Rabbinge (1976: *Panonychus ulmi - Amblyseius potentillae*), Wollkind & Logan (1978: *Tetranychus mcdanieli - Metaseiulus occidentalis*) and Dover et al. (1979: *Panonychus ulmi - Amblyseius fallacis*).

The model of Fransz (1974) is based on a component analysis of the predatory behaviour of *Metaseiulus occidentalis*: it simulates the rate of predation on prey eggs and prey males distributed over a small bean-leaf disc. Rabbinge (1976) and Wollkind & Logan (1978) based their population model of the predator-prey interaction on measurements at the individual level of life history traits and the rate of predation. By using small leaf-discs the interaction surface is easily defined and prey density can be directly assessed as long as the prey is randomly distributed over the disc. In this way variables like the rate of predation and the rate of reproduction by the predator were measured in relation to the density of the prey.

The latter authors simulated the predator-prey interactions in larger ecosystems (e.g. the orchard) by simple extrapolation of the measurements on the leaf-discs to the surface of the ecosystem, e.g.

$$\frac{5 \text{ prey eggs}}{1 \text{ cm}^2} = \frac{5 \cdot 10^{12} \text{ eggs}}{1 \cdot 10^{12} \text{ cm}^2}$$

This assumes that the prey is randomly distributed and that the predator searches for prey in a random fashion. But the distribution of tetranychids in the field as well as in the greenhouse crops is generally clustered (e.g. Croft et al., 1976) and as it is likely that predators tend to aggregate at prey colonies, it is relevant to include these aspects for the understanding of the population fluctuations of predator and prey.

Dover et al. (1979) recognized this problem. They directly monitored the result of the dispersal process in the practical situation of the orchard by counting the number of prey mites and predatory mites on each leaf of a representative sample of leaves. These mite counts were used to create separate frequency distributions for predator and prey. An appropriate two-parameter model, the negative binomial distribution, was used for description of the frequencies. By assuming the independence of the predator and prey distributions, their descriptive models were related to each other in a joint probability function. This function was used in a predator-prey model to account for predators occupying leaves at below-mean or above-mean prey densities. However, this implies that each leaf has the same probability of containing a given number predators, irrespective of the number of prey. Whether or not this is true, it remains difficult to understand how the - presumably prey-density related - predation and dispersal give rise to a dispersion that can be described by a negative binomial function. Moreover, by representing the predator-prey distribution by frequency distributions, the positions of the colonies and the leaves with respect to each other are not considered, so that the spatial mosaic of predator and prey colonies is eliminated as an aspect of predator-prey interaction.

None of the above models include the dispersal mechanisms of predator and prey in relation to the heterogeneity of the environment. These factors can affect the persistence of prey and predator populations in an ecosystem, as shown by Huffaker (1958) in an experimental study of the interaction between a predatory mite (*Metaseiulus occidentalis*) and a spider mite (*Eotetranychus sexmaculatus*) in artificial universes differing in complexity. He constructed an environment of interconnected oranges that were suitable as a food source for the prey. Some days after the introduction of the spider mites on their substrate, the predators were released. They exterminated the spider mites within a month. Apparently the predators were able to cover the whole substrate in search of prey. However, when these walking predators were prevented from dispersing, using vaseline barriers, and prey dispersal by 'ballooning' was stimulated with low-velocity air currents, prey and predator survived for six months in this artificial ecosystem. Therefore more detailed modelling and experimentation are needed to elucidate the role of dispersal and heterogeneity in the population dynamics of predator and prey.

Factors that have to be taken into account, are for example: the influence of degree of rose-crop heterogeneity, the effect of prey and predator density on the residence time of the predator in a prey colony and the time spent outside the prey colonies by the predators. In addition a model is needed in which the dispersal mechanisms are specifically incorporated and the predator and prey distributions are generated in space. But such a complex model requires a lot of computing time. It would be desirable to use a simpler, less time-consuming model. However, it is not possible to make a-priori statements on the relative importance of dispersal mechanisms in predator-prey models. It is known that the model proposed by Dover et al.

(1979), in which field measured dispersion parameters of the negative binomial account for the degree of coincidence between predator and prey give results that differ considerably from simulations that do not take dispersion into account. Because this difference is more a demonstration of the static structure of their model than a proof of the importance of the low degree of coincidence between predator and prey, it shows once more the need for further research on this matter.

Another aspect of the distribution of *Tetranychus* spp. that is not considered in most studies of the functional response and in the modelling study of Wollkind & Logan (1978), is that these spider mites aggregate within structures of self-made webbing, in contrast to *Panonychus* spp., which predominantly spin 'lifelines' made of silk strands. As the predator-prey interaction takes place only where there are aggregations, prey abundance should be quantified as the number of mites per webbed leaf area, instead of per total leaf area. Moreover, webbing may play an important role in searching and predation, as indicated by experiments of McMurtry & Johnson (1968), Fransz (1974), Takafuji & Chant (1976) and Schmidt (1976).

Still other factors may contribute to the lack of conformity between laboratory and greenhouse experiments, e.g. effects of spider-mite crowding during hostplant exploitation and availability of alternate food sources in periods of prey scarcity. A final difference between laboratory and greenhouse conditions can be found in their microclimates. First, temperature plays a very important role in the population dynamics of poikilotherm arthropods. For example, a rise in temperature enhances development, stimulates reproduction and increases food consumption. Although a greenhouse in, say, Aalsmeer may seem a well-regulated climatic environment, this is only partially true. As a consequence of the variability of the outdoor climate and despite of the 'between limits' regulation of the glasshouse climate, temperatures range between 10°C and 33°C. Because of this variability, temperature has to be measured to enable validation of predator-prey models, which incorporate several temperature-dependent variables. However this raises a problem with respect to the microclimatic detail needed. As rose leaves are rather dark objects, leaf temperature may differ from the air temperature, depending on the amount of incident (hedge-penetrating) radiation. Due to the small size of the mites (<1 mm) their environmental temperature will be determined to an important extent by the leaf. Goudriaan (1977) has presented a simulation model that calculates the leaf temperature distribution in a canopy on the basis of the weather conditions above the canopy, the crop geometry, the optical properties of the leaf and the behaviour of the leaf stomata. This model can be coupled to a model of arthropod growth (Rabbinge, 1976). Even correction for interception of radiation by the structural elements of a greenhouse can be made, as shown by Kozai et al. (1978).

Unlike the leaf temperature, the humidity near to the leaf cannot be computed or directly measured. Moreover, tetranychid webbing covers the underside of the leaf and this may interfere with the microclimate (Hazan et al., 1975b). This problem can be eliminated to some extent by using webbed leaves of intact plants in controlled humidity cabinets in laboratory experiments. The extrapolation of these measurements to the greenhouse situation can be accomplished via intra-crop humidity profiles, which can be calculated from the above-crop weather conditions using Goudriaan's model. Although the above-crop weather conditions would have to be measured continuously, other data for the model, such as the geometrical, optical and physiological properties of the leaves, would only have to be measured once for intra-crop extrapolation.

1.4 MODELLING OF THE PREDATOR-PREY SYSTEM

In modelling a complex system it is advisable to distinguish only two levels of causal depth (van Keulen, 1975). Therefore the study described in two reports attempts to explain the population fluctuations of predator and prey in the greenhouse (Part 2) on the basis of laboratory experiments at the individual level (Part 1). The life history parameters (development, reproduction, mortality and sex ratio; Part 1 Chapter 2) and the predator-prey interaction (predation and dispersal behaviour; Part 1 Chapter 3) were measured by studying individual mites in the laboratory. The data obtained were fed into a model that computes population growth and generates dispersion patterns in space (Part 2).

These extrapolations to the population level were validated by comparison with actual population experiments in the greenhouse. From the discrepancies, indications were derived for improving the model. Additional measurements were taken and the modelling and validation procedure repeated. This working procedure offered a framework for the evaluation of the phytoseiid predators, in particular for greenhouse culture of ornamental roses. These phytoseiid species were compared for each laboratory experiment on the individual level and the impact of these differences on the final objective, 'biological control', was evaluated with model calculations described in Part 2.

In the acarine predator-prey system the causal relations are manifold. However, some parts of the system contain more interconnections between variables than others. These parts are called submodels. The structure of the acarine predator-prey system was subdivided into four levels. The first level concerns the ability of the predator to locate its prey at some prey density and at a well-defined motivational state of the predator (Level 1). Motivation is not constant, but depends on the feeding history and the food conversion (e.g. Fransz, 1974). Incorporating the dynamics of the motivational state leads to the subsequent level of complexity (Level 2). Due to predation, but also reproduction, abiotic mortality, development, etc., prey and predator numbers will change during the interaction period; incorporating this adds another dimension to the predator-prey system (Level 3). Finally the prey aggregate in colonies. As new colonies are founded, the predators may move from one colony to the other. This emphasizes the final level of complexity, the dispersal of the predator (Level 4).

These four levels are recognizable in the population model as submodels that simulate the relative rate of successful encounter at some level of the motivational state, the rate of predation at some level of the prey density, the population growth per prey colony, the rate of departure from the prey colony and the redistribution of the dispersing mites over the substrate (e.g. prey colonies in case of the predator and leaf surface in case of the prey). After validating all submodels separately, predictions were obtained from the entire model, which were themselves again validated by experiment.

The model is of the state-variable type (Forrester, 1961); state and rate variables are distinguished and mathematical expressions are given to calculate the value of each rate variable from the state of the system. Examples of state variables are the number of eggs, the motivational state of the predator, etc. The rate of egg development, the oviposition rate and the predation rate are examples of some of the rate variables. The state variables are updated by rectilinear integration over a sufficiently short time interval:

$$Y_{t+\Delta t} = Y_t + RY \cdot \Delta t$$

$$RY = Y_t \cdot RRY$$

t = time (e.g. day)

Δt = time interval of integration

Y = state variable (e.g. number)

RY = rate variable (e.g. number per day)

RRY = relative rate (e.g. day^{-1})

Unfortunately integration methods that continuously adjust the time interval of integration on the basis of some accuracy criterion (e.g. Runge-Kutta/ Simpson) cannot be used in the population program. The method for the simulation of dispersion in developmental time (the 'boxcar' method; Goudriaan, 1973) requires the use of retilinear integration, because some of the rate variables involve a division by Δt (= discontinuous emptying of a 'boxcar'; de Wit & Goudriaan 1978, p. 20). Therefore the size of the time interval of integration has to be prefixed. As a rule of thumb it has to be smaller than 20% of the time constant of the integration process (Ferrari 1978, p. 26). The inverse of the time constant equals part of the rate RY that is independent of Y. For the simple integration above the time constant equals the inverse of RRY.

When the model consists of a system of integrals, the time constant of this system is governed by the integration with the smallest time constant. to evaluate a number of natural enemies for the biological control of arthropod pests.

Because the time constants of different processes treated in a simulation model often differ considerably, the computing effort is inefficient for the integration of the slow processes. This problem will be encountered in Part 2 with respect to the adaptation of the motivational state of the predator to a continually changing prey abundance in time and space. Numerical integration of difference equations over short time intervals is applied because of the complex character of the interactions. For example, the rate of successful encounter of the predator with its prey and the preference of the predator for the different stages of the prey depends on its feeding history. Moreover, temperature influences several rate variables and it varies continuously during population growth in the greenhouse. The addition of non-linear terms to the differential equations often prevents solution by analytical techniques. Numerical methods are the only solution in that case.Even when the system consists of only linear differential equations, the large number of these equations necessitates the use of numerical techniques (see e.g. Hall & Day 1977, p. 10).

The use of random numbers to simulate the stochastic character of a variable is not necessarily implied. Most parts of the model have a deterministic character. However there are some situations in which the stochastic nature of a variable is absolutely basic to the proper modelling of the process. Fransz (1974) demonstrated that even when one is only interested in mean values, deterministic models of the predation process can lead to results different from those of stochastic models when non-linear relations between the rate and state variables of the model are involved. In the model described in this report Monte Carlo procedures are applied to simulate the predatory mites' walking behaviour (Part 1, Subsection 3.2.4) and capture events (Part 1, Subsection 3.3.1). Because of the large amount of replicates needed to obtain a reasonable estimate of the mean rate of predation these inefficient Monte Carlo procedures were replaced by more economical alternatives whenever possible. For example, the Monte Carlo simulations of the predation process were compared with several alternative models that are based on a larger set of assumptions but are much more efficient in terms of computing effort (e.g. compound simulation, Fransz 1974; queueing approach, Curry & DeMichele 1977).

Mathematical formulation of the interacting growth processes forces the investigator to measure the biological components of the system in such a way that they fit the context of the model. Subsequently, the importance of the input data relative to each other can be determined by studying the overall effect of a standard perturbation of a parameter value in the model. This so called sensitivity analysis gives an indication of the required accuracy of the input data and thus of the number of replicates needed to obtain this accuracy at the 5% level (e.g. Cochran 1963, p. 73-77). Both the investigation of the relative importance of the variables involved and the assessment of the required accuracy of the inputs may make it feasible

2 Bionomics of prey and predator

The framework of a model of arthropod population growth consists of stage-specific rates of development and survival, and age (or state) specific rates of reproduction, sex ratio in the offspring and senescence. Such life-history frameworks can be modelled for both prey and predator and subsequently coupled by prey stage-specific predation rates of each stage of the predator (Part 2).

Rates of predation will depend on prey abundance, which, therefore, has to be quantified. The interference between *Tetranychus* spp. and their predators takes place on those parts of the leaf area that are covered with webbing, since all stages of the spider mite are aggregated there. To quantify prey abundance therefore, it is more logical to define prey density as the number of prey per square centimetre of webbed leaf, rather than per leaf area, as Wollkind & Logan (1978) did. The size of the webbed area changes during population growth, as do the prey numbers. Therefore both the rate of population increase and the rate of increase of webbed leaf area should be measured to calculate the prey density in the computer simulation model. In this chapter a complete picture is given of the life histories, webbing activity and stage-specific rates of predation, as affected by arthropod related factors (stage of development, age of the adult, etc.) and environmental factors (temperature, relative humidity and food supply). These measurements are part of the input to the population models presented and validated in Part 2, but they are also basic to the structure of these models.

In the final part of this chapter the ability of the predator to survive periods of spider-mite scarcity and to recover from starvation are determined. This is important in assessing possible alternative foods for maintaining a predator population in a greenhouse crop in absence of spider mites.

2.1 TETRANYCHID PREY

The life history traits of *Tetranychus urticae* on rose (*Rosa canina* 'Sonia', grafted on *Rosa indica* 'Manetti') are discussed in Subsections 2.1.1 - 2.1.3. Although much life history data are available from literature, new measurements were made because variation due to differences in mite strain (e.g. Lehr & Smith, 1957), host plant (e.g. Dabrowski & Marczak, 1972) and even cultivar involved (e.g. Bengston, 1970; Tulisalo, 1971; de

Ponti, 1978) can be considerable. The strain of *Tetranychus urticae* used throughout this investigation originated from a culture maintained at the Research Station of Floriculture at Aalsmeer, where it was collected from greenhouse roses and reared for several generations on beans (*Phaseolus vulgaris*, 'Stamkievitsboon').

Jesiotr & Suski (1976, 1979) found a difference in reproductive potential between mites fed on beans and those fed on rose 'Baccara'. After transfer of the mite population from rose to bean or vice versa these differences were observed over a period of more than one generation, which may suggest adaptation of the population to the new host plant through selection. Because it was more practical to cultivate the spider mites on beans than on roses, in addition to rose 'Sonia' the bean 'Noord-Hollandse Bruine' is also considered as a host plant.

The food turnover of *Tetranychus urticae* is considered to enable comparison of the conversion efficiencies of the plant-feeding spider mites and the mite-feeding predatory mites (Subsection 2.1.4). Furthermore, the role of the webbing is discussed, especially in relation to the phytoseiid predators (Subsection 2.1.5). The web production and the growth of the webbed area is quantified to enable the calculation of prey density (Subsection 2.1.6).

The following aspects of the bionomics of Tetranychidae will be discussed only briefly:

Food quality of the host plant for the parenchym feeding spider mite
The food quality of the host plant, as affected by plant nutrition, is considered to be constant under practical circumstances of cultivation. For example, the N, P and K levels of rose leaves are mostly within 10% of their mean levels (Arnold Bik, personal communication), which is a small variation relative to their effect on the reproduction of *Tetranychus urticae* (Rodriguez, 1964).

Fertilization status of prey and predator Females of tetranychid and phytoseiid species sampled in the field are rarely unfertilized. Potter (1976a, 1978) and Blommers & Arendonk (1979) review several explanations for this phenomenon.

Extreme temperature and relative humidity In the greenhouse culture of ornamental roses temperatures normally range between 10°C and 33°C, while relative humidities range between 45% and 90%. These ranges are based on measurements at 40 locations spread over the rose-growing area of The Netherlands (van Rijssel, personal communication).

Wind and rain Glasshouse structures nullify effects of wind and rain.

To restrict the amount of work involved in this study, several aspects that influence the predator-prey system have been purposely neglected, despite their importance for the effectiveness of control:

Implications of chemical spraying The toxic effects of several compounds to both predator and prey are being studied by van de Vrie (Research Station of Floriculture, Aalsmeer) and van Zon (University of Amsterdam, Amsterdam).

Diapause, as a means to survive the winterperiod The induction as well as the termination of the diapause of the two-spotted spider mite and the phytoseiid predator depend on photo-period, temperature and the availability of food. In addition to the literature reviewed by van de Vrie et al. (1972) and McMurtry et al. (1970), the following references represent current knowledge on this topic:
-*Tetranychus urticae*: Geispits et al., 1971;Hussey, 1972; French & Ludlam, 1973; Helle & Overmeer, 1973; Fritzsche & Lehman, 1975; Veerman, 1977a,b.
-Phytoseiidae: Sapozhnikova, 1964; Boczek et al., 1970; Hoy & Flaherty, 1970; Wysoki & Swirski, 1971; Knisley & Swift, 1971; Rock et al., 1971; Croft, 1971; Hoy, 1975a,b; Simova, 1976; Hamamura et al., 1976b.

2.1.1 Development and mortality

The rate of development and juvenile mortality was measured in a serial thermal cabinet at constant temperatures of 13, 15, 20, 25, 30 and 35°C; the relative humidity ranged between 55% at 35°C and 85% at 15°C. The leaves of the host plant were placed upside down on a wet sponge floating in a plastic box filled with water. These leaves were covered with water-soaked tissue paper that had been perforated at regular distances with a leaf puncher. In that way circular parts of leaves were obtained that were surrounded by wet tissue, which acted as a barrier for all stages of spider mites. The justification for the use of detached leaf cultures in life-table studies was given by Rodriguez (1953), de Ponti (1977b) and Dąbrowski & Bielak (1978).

The eggs, used to start the experiments, were deposited within a one-hour period. The subsequent progress in development and the juvenile mortality were observed at intervals of eight hours at all temperatures. The transfer to fresh leaves, which is necessary to eliminate effects of diminishing food quality was carried out at least every 3 days, but only if the mites were in a mobile stage.

To study the effect of alternating temperatures on development, some of the experimental boxes were transferred at daily intervals from 10°C to 20°C and vice versa in one series, and in another series from 25 to 35°C. The developmental time from the deposition of the egg until first reproduction ('egg-to-egg' development) is plotted in Fig. 4. The rate of development

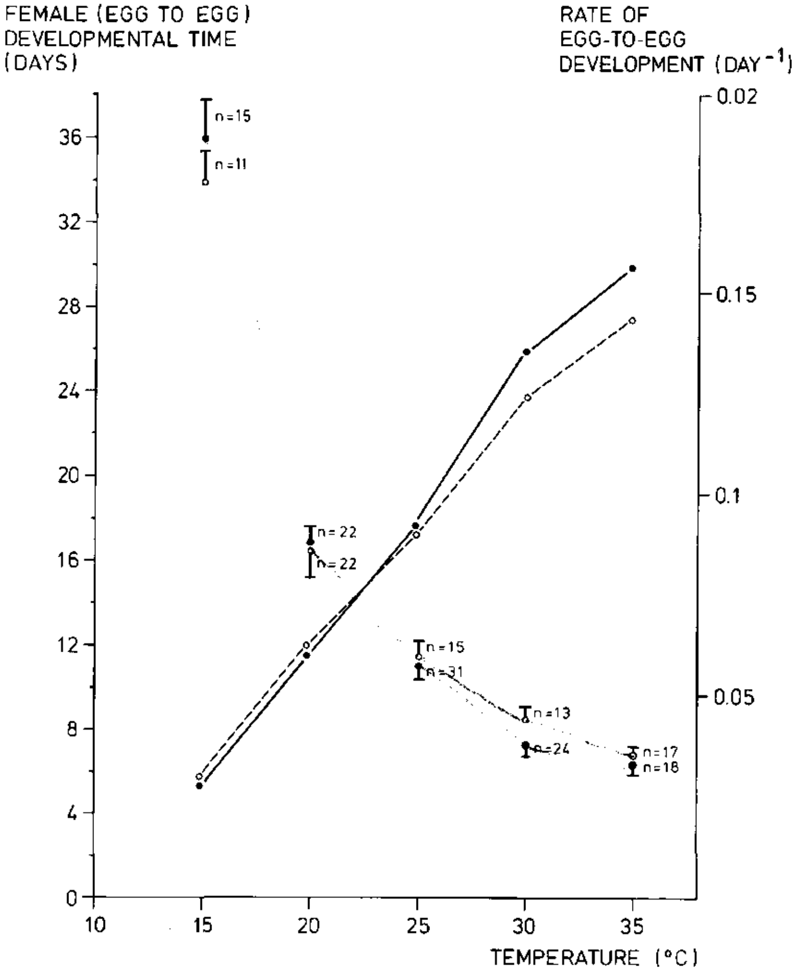


Fig. 4. Means and standard deviations (⊥, n = number of replicates) of 'egg-to-egg' developmental times of *Tetranychus urticae* on bean (o) and rose (●) at constant temperatures. The drawn lines represent the rate of 'egg-to-egg' development.

the inverse of developmental time) depends linearly on temperature (15-35°C), a general phenomenon in Tetranychidae. A Student's t-test for comparison of two means and an F-test for comparison of their respective variances did not reveal significant differences between developmental time at the above mentioned alternating temperatures (10-20°C and 25-35°C) and that simulated on basis of the measurements at constant temperatures (Table 1) and a modelling technique (Part 2) at the 5% level. Therefore the rate of development may be considered as reacting instantaneously to a change in temperature. This was also found for other Tetranychidae, like *Panonychus ulmi* (Rabbinge, 1976) and *Tetranychus mcdanieli* (Tanigoshi et al., 1976).

Table 1. The effect of alternating temperatures on 'egg-to-egg' developmental time (hours) of females of *Tetranychus urticae*.

Interpolation[a]		Simulation[b]		Observation		n	Temperature alternation
$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$		
193.7	15.0	196.2	14.4	198.1	12.4	28	25-35°C
663.8	55.5	671.9	51.0	677.8	48.1	24	10-20°C

a. Developmental time (= DR) estimated by linear interpolation from the measurements obtained at constant temperatures e.g. $[(DR_{10} + DR_{20})/2]^{-1}$.
b. Simulated by the population model presented in Part 2 of this Agricultural Research Report (to be published) using measurements obtained at constant temperatures.

In Table 2 the developmental times are given per stage and sex. The relative length of the different stages as a part of the total egg-to-egg developmental period is rather constant, irrespective of the temperature: egg 39%, larva 9.5%, protochrysalis 8%, protonymph 7%, deutochrysalis 8%, deutonymph 8.5%, teleiochrysalis 11% and pre-oviposition female 9%.

Although the rate of development is strongly affected by temperature, mortality remains constant at a low level (about 10% from egg to adult) in the range 15-30°C (Table 3). Outside this temperature range mortality increases, as was also found by Mori (1961), Stenseth (1965) and Nickel (1960). Assuming that at each moment during the developmental period a constant proportion of the mites die from a non-predator cause, the relative rate of mortality can be computed as follows:

$$RRM = \frac{-\ln(N_t/N_o)}{t} = -\ln(M)\cdot DR$$

RRM = the relative rate of mortality (day^{-1})
N_t = the number of mites at time t
t = the developmental period (day)
DR = rate of development (day^{-1})
M = mortality

The stage-specific mortalities are incorporated in the population models presented in Part 2 by using these relative rates.

Several studies have shown that both low and extremely high humidity causes an increase in juvenile mortality and retards development (Boudreaux, 1958; Ferro & Chapman, 1979; *Harrison & Smith*, 1961; *Hazan* et al., 1973;

Table 2. Female and male developmental time (hours) of *Tetranychus urticae.*

Temperature (°C)	Stage of development																Total		n
	E		L		PC		PN		DC		DN		TC		PF				
	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	
Females																			
13	648	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
15	342	18	90	14	70	9	61	10	65	9	73	13	85	9	84	21	870	38	15
20	160	4	36	6	31	4	27	6	29	5	34	5	40	5	41	8	398	21	22
25	103	2	24	9	21	4	17	6	21	5	23	4	31	6	21	5	261	14	31
30	68	5	17	5	14	5	13	5	15	8	14	6	20	6	15	4	176	13	24
35	56	3	15	2	11	4	11	4	11	4	19	7	17	4	14	5	154	16	18
Males																			
13	640	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
15	341	14	106	31	69	7	52	10	68	11	50	7	80	6	-	-	766	45	11
20	161	1	34	3	33	5	24	5	30	5	26	6	38	4	-	-	346	12	14
25	104	2	19	4	24	5	14	4	21	6	16	5	27	4	-	-	225	7	7
30	71	4	14	5	13	5	12	4	13	4	11	4	17	3	-	-	151	11	11
35	59	2	11	4	12	4	10	4	13	6	12	6	16	7	-	-	133	9	9

E = egg
L = larva
PC = protochrysalis
PN = protonymph
DC = deutochrysalis
DN = deutonymph
TC = teleiochrysalis
PF = preovipositional female
n = number of replicates

Table 3. Mortality (%) in the developmental stages of *Tetranychus urticae.*

Temperature (°C)	Stage of development								Total	n
	E	L	PC	PN	DC	DN	TC	PF		
10	15.6	12.5	-	-	-	-	-	-	38.4	190
15	6.1	1.4	1.0	1.0	0.0	2.2	0.0	0.0	11.3	154
20	6.3	1.1	0.0	1.3	0.0	0.0	1.0	0.0	9.6	181
25	4.3	1.9	0.0	0.0	0.0	1.0	1.0	1.5	9.3	144
30	6.6	1.4	1.2	0.0	1.0	0.0	0.0	1.0	10.8	100
35	10.1	4.1	0.0	2.9	1.0	2.1	3.0	4.0	24.4	144

Abbreviations are explained in Table 2.

McEnroe, 1963; Nickel, 1960). However the range of humidities for which development is not affected differs from study to study. Hazan found optimal conditions for *Tetranychus cinnabarinus* at a relative humidity of 38%, but Harrison & Smith found little differences in egg development of *Tetranychus urticae* in the range 50-90%, and showed that the egg mortality at 100% relative humidity occurred only after 6 days of exposure. Because such high humidities occur for only short periods under greenhouse conditions (van Rijssel, Research Station of Floriculture, Aalsmeer; personal communication) this effect is ruled out as a factor of importance. Moreover, an experiment carried out for a more realistic range of humidities (50%, 75% and 85% at 23°C) did not reveal any difference in development or mortality (Table 4). A possible explanation for the absence of any reaction is that these experiments were carried out on webbed leaves that were connected to a part of their shoot, for, as postulated by Hazan et al. (1975b), both webbing and defaecation by the spider mite and, probably most important of all, evapotranspiration by the leaf may act as a buffer to changes in humidity. For this reason humidity is not important under the greenhouse conditions (relative humidity 45-90%) in The Netherlands.

To study the effects of transferring spider mites from bean to rose, simultaneous experiments on both host plants were carried out. The results are given in Fig. 4. A t-test for comparison of means and F-test for comparison of variances did not reveal significant differences at the 5% level between development on bean and rose. To check if this conclusion also holds after generations of feeding on the same host plant, another comparison was made after a six-month culturing period. The results (Table 9) show that in contrast to the results of Jesiotr & Suski (1976) with bean and rose 'Baccara', the present cultivars of bean and rose 'Sonia' are interchangeable host plants with respect to developmental time.

But for one exception (Marle, 1951), data from literature about developmental time on several bean cultivars are in close agreement (Gasser, 1951; Hussey et al., 1957; Bravenboer, 1959; Fritzsche, 1959; Nickel, 1960; Suski

Table 4. The effect of relative humidity (T = 23°C) on female 'egg-to-egg' developmental time of *Tetranychus urticae*.

Humidity (%)	Developmental time (hours)		
	$\hat{\mu}$	$\hat{\sigma}$	n
45-50	286	17	44
70-75	289	19	52
85-90	292	21	48

& Badowska, 1975; Shih et al., 1976; Saito, 1979b; Feldmann, 1981). Comparable data about developmental time on greenhouse roses are not available. As for developmental time, juvenile mortality may differ with the plant species or cultivar (Dabrowski & Marczak, 1972). Tulisalo (1969) found differences in juvenile mortality between cultures grown on different cultivars of cucumber, although the rate of development did not differ significantly. However, in the study described in this report juvenile mortality was very low on both host plants (bean and rose), which corresponds with the results given in the above-mentioned literature, except for Shih et al., who reported a rather high mortality (30%).

Of the vast number of studies on nutrition in Acarina, only that of Suski & Badowska (1975) concerned the influence of NPK supply on the rate of development and the juvenile mortality. The relations they established are complex. It is sufficient to mention here that the nutritional ranges used in the experiments caused changes in the rate of development and juvenile mortality that were within 15% of mean values. However the nutritional range was probably larger than that found in practical agriculture. The nutrient composition of the leaf may also be affected by its ageing; no experimental evidence of an effect on the rate of development was found, however (Table 10).

During mite-colony growth the eggs and juveniles are left stranded in already exploited leaf areas. The young mites are not as active as the mature mites, which may cause mortality additional to that measured in the previous experiments, where the mites were cultivated individually on fresh leaves. Wrensch & Young (1978) measured a marked reduction in rate of development and survival at high spider-mite densities. However, as they confined the mites to a leaf disc, the importance of intraspecific competition for food still has to be demonstrated. Spider mites are able to control their density (number of mites per square centimetre webbed leaf area) partly by increasing the webbed area and partly by dispersal. To decide whether these factors need to be studied in more detail, a greenhouse experiment on population growth was carried out and the numerical results were compared with simulations of the same experiment, which neglect effects of intraspecific competition. This experiment will be discussed in Part 2.

2.1.2 Reproduction and life span

Experiments on the rate of reproduction and ageing were carried out using a similar experimental design as that described in the previous subsection (Subsection 2.1.1). Fifty female deutonymphs close to their final moult were sampled for each trial. Males were introduced to guarantee immediate insemination of the female after eclosion. The number of eggs were recorded and removed at eight-hour intervals. Moreover, female mortality was registered, ignoring deaths by unnatural causes, e.g. drowning in the water-soaked tis-

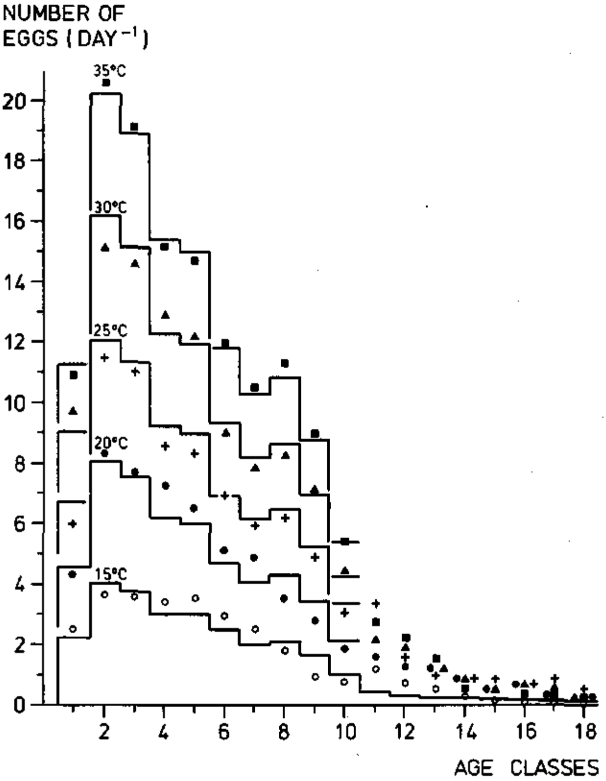


Fig. 5. Rate of reproduction of *Tetranychus urticae* in relation to female age class and temperature. The histogram visualizes the descriptive power of the intra-age class regressions. Length of each age class at different temperatures: 3.5 day at 15°C; 2.5 day at 20°C; 2.0 day at 25°C; 1.25 day at 30°C; 1.0 day at 35°C.

sue (5-10%). Because both reproduction and mortality appeared to depend on age, the data were classified in age periods forming equal parts of the maximum life span. This maximum longevity of the female was estimated via a least-squares estimate of the 97-99% point of the cumulative frequency distribution of life spans, plotted on probability paper of the Gaussian distribution. From this linear relation the mortality per age class was estimated. This mortality together with the duration of the classified age periods was used to calculate the relative rate of mortality. This classification approach requires some degree of intra-class constancy of the relative rate variables involved. For this reason the maximum life span was divided in 18 age classes, preceded by a pre-oviposition period. The duration of the age periods and the age-dependent rate of reproduction in relation to temperature are given in Fig. 5. It appeared that the intra-class rate of reproduction in the initial 10 age classes depends on temperature

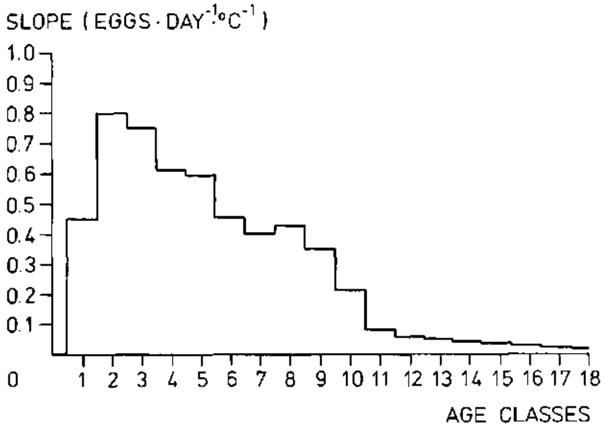


Fig. 6. Slope of the oviposition rate (eggs·day^{-1}·°C^{-1}) in relation to the age class. Slope = oviposition rate/(temperature - 10°C).

Table 5. Potential and net fecundity of *Tetranychus urticae* in relation to temperature.

Temperature (°C)	Fecundity				
	potential[a]	net[b]			
	$\hat{\mu}$	$\hat{\mu}$	$\hat{\sigma}$	n	range
10	31.2	28.6	9.8	48	6- 44
15	98.0	84.2	36.6	43	35-170
20	146.2	129.9	53.3	42	43-272
25	160.8	129.7	48.9	45	41-237
30	135.3	119.5	33.7	38	40-185
35	135.4	120.6	38.6	39	40-177
10-20	101.1	87.5	28.8	41	35-157
25-35	148.3	123.9	40.8	38	43-205

a. Potential fecundity = total number of eggs produced per female, excluding age-dependent mortality.

b. Net fecundity = total number of eggs produced per female, including age-dependent mortality.

in a linear fashion over the whole temperature range from 15°C to 35°C. This enabled a more concise description via the slopes of the linear regression lines, which cross the x axis close to 10°C. These tangents of the angle of inclination are plotted in Fig. 6 and their descriptive power is visualized by the histograms in the original graph of the age-specific rates of oviposition (Fig. 5).

In Table 5 the mean egg production per female is given as a net (= female mortality included) and a potential (= female mortality excluded) fecundity, which shows that mortality causes only a 10-20% decrease of the fecundity relative to the potential. Fecundity appears to be unaffected by temperature over a rather large range (20-35°C). However below 20°C it decreases, being 70% at 15°C and 20% at 11°C.

The mean and maximum life-spans depend on temperature in a much more gradual way, as can be seen in Table 6 and Fig. 5. Because the post-oviposition period is absent or very short, the adult life-span is only subdivided in a pre-oviposition period and a post-oviposition period.

As with reproduction, survival may depend on temperature and ageing, i.e. the age relative to the maximum life-span. Therefore the relative rate of mortality was determined for each age class and at all experimental temperatures. From simulations of population growth (Part 2), it appears that the numerical effects of the temperature dependency could be neglected as well (12-35°C). For this reason the relative rates were smoothed out by repeated simulation of the above survival and reproduction experiment until an acceptable overall fit was found. These fitted values are given in Table 7. They demonstrate that the relative rate of mortality depends on the age relative to the maximum life-span.

Table 6. The length of the preoviposition and oviposition period (days) of *Tetranychus urticae*.

Temperature (°C)	Preoviposition period			Oviposition period			
	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n	range
10	25.00	-	20	100	-	48	28-
15	3.49	0.87	15	39.3	14.5	43	12-67
20	1.70	0.32	22	26.5	8.1	42	13-44
25	0.89	0.20	31	21.8	8.8	45	8-48
30	0.61	0.16	24	11.6	3.2	38	8-20
35	0.60	0.20	18	10.6	2.6	39	6-16
10-20	3.05	0.91	22	40.6	10.0	41	16-59
25-35	0.55	0.11	28	13.4	5.1	38	6-31

Table 7. The smoothed estimates of the relative mortality rate (day^{-1}) of *Tetranychus urticae* in relation to the age class of the adult female.

Female age class													
1-5	6	7	8	9	10	11	12	13	14	15	16	17	18
0.0	0.002	0.02	0.05	0.05	0.07	0.10	0.10	0.10	0.10	0.15	0.15	0.30	0.50

Table 8. The effect of humidity (T = 23°C) on net fecundity and oviposition period of *Tetranychus urticae.*

Relative humidity (%)	Net fecundity		Oviposition period (days)		n
	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	
45-50	130.1	44.0	23.1	9.2	26
70-75	129.8	45.1	23.6	7.9	34
85-90	122.4	38.2	22.4	7.1	30

The effect of humidity on the rate of reproduction was analysed by Boudreaux (1958), Nickel (1960) and Hazan et al. (1973). The oviposition rate is maximal for relative humidities below 90%, the maximum depending on temperature and the species involved; Hazan et al. (1973) found optimal values at relative humidities of 22-38%. Above 90% relative humidity the oviposition is lowest. As argued in the previous subsection the humidity near to a webbed leaf will probably differ from the environmental relative humidity at the same temperature due to evapotranspiration of the leaf and defecation by the spider mite. To study the effect of the humidity buffering capacity of the webbed leaves mite reproduction was measured on this substrate at three humidity levels (relative humidity = 50, 75, 85% at 23°C) for the same experimental design as discussed in Subsection 2.1.1. The results (Table 8) indicate that as for the rate of development, humidity is ruled out as a factor of importance for the reproduction of *Tetranychus urticae* within the humidity range of practical interest.

As with the rate of development, fecundity was measured also on both rose 'Sonia' and bean 'Noord-Hollandse Bruine' (Table 9). These trials were done with spider mites cultivated previously on bean and were repeated with mites cultivated for six months on rose. Both t-test and F-test for comparison of means and variances, respectively, did not reveal significant differences at the 5% level. Therefore it is probable that these particular

Table 9. The effect of the culturing period on some life-history traits of *Tetranychus urticae* (T = 25°C).

Phase of culturing	Female 'egg-to-egg' developmental time (hours)			Net fecundity			Oviposition period (days)		
	n	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$
directly after transfer to rose	31	261	14	45	129.7	48.9	45	21.8	8.8
after a 6-month period of culturing on rose ('Sonia')	42	266	16	40	132.1	47.3	40	21.5	8.1
continuously cultured on bean ('Noord-Hollandse Bruine')	15	270	21	41	133.4	50.8	41	22.2	9.2

cultivars of bean and rose are interchangeable host plants with respect to the life-traits studied.

Comparison of these results on rose with data from the literature on bean shows similar fecundity levels (Bravenboer, 1959; Lehr & Smith, 1957 (Massachusets strain); van de Bund & Helle, 1960; Watson, 1964 (old leaves); Suski & Badowska, 1975; Shih et al., 1976; Saito, 1979b; Feldmann, 1981) with only a few lower values (Gasser, 1951 - 68 eggs; Lehr & Smith, 1957 (Canterbury strain) - 107 eggs; Fritzsche, 1959 - 57-80 eggs) and higher values (Watson, 1964) (young leaves). At other host plants fecundity levels similar to the present results may be obtained, but mostly lower levels are reported.

In several cases the chemical composition of the plant has been shown to correlate with mite fecundity. According to Jesiotr & Suski (1974) fecundity of the two-spotted spider mite is lower on rose 'Baccara' than on a number of other rose cultivars. However Dabrowski & Bielak (1978), who studied nutritional correlations with mite reproduction in 4 cultivars of both ornamental roses, were not able to explain this result; they only found some correlation with the content of glutamic acid. Furthermore, they found a positive correlation with the total nitrogen content and total free endogeneous amino acids. According to the review by Suski & Badowska (1975) the effect of nitrogen is often positive, but the results with potassium and phosphorus are far from conclusive. Suski et al. (1975) state that the extreme conditions produced in the nutritional solutions in the laboratory are rarely met in practice today and therefore the effects on mite reproduction reported can be ignored. Moreover, the role of adaptation of a mite population to modified nutritional conditions, as indicated by the results of Jesiotr & Suski (1974), is virtually overlooked in the laboratory experiments, where generally instantaneous, instead of delayed responses (> 1 generations) to nutritional changes are measured. Because in practical rose culture today more or less constant NPK levels are maintained, and because the genetic make-up of the greenhouse populations seems to be rather stable, which indicates minor exchange with outdoor mite populations (Overmeer et al., 1975), it may not be far from reality to consider the nutritional conditions as a constant or an implicit 'noise' factor. This assumption is supported by the fact that in practice NPK levels of 'Sonia' rose leaves (3.10% N, 0.28% K, 2.20% P) are largely within 10% of their mean values, so that in most cases fecundity varies within 11% of its mean level (Rodriguez, 1964). Rabbinge (1976) came to the very same conclusion for the fruit-tree red spider mite, which infests Dutch apple orchards.

Besides fertilizer doses, the nutrient composition may also be influenced by the age of the leaf or by seasonal changes (e.g. Storms, 1969; Dabrowski, 1976). However the age of 'Sonia' leaves is probably not of importance: female spider mites placed on green leaves at the top, middle or lower part of a rose bush produced a similar amount of eggs (Table 10). Besides, yellowing leaves are dropped rather soon and these senescent leaves are simply left or avoided by the spider mites. Seasonal changes in food quality were not studied.

Food quantity is affected by feeding of the spider mites. The available leaf parenchym decreases during population growth until the host plant is exhausted. The overall damage may exceed the direct damage done to the host

Table 10. The influence of leaf age on some life-history traits (T = 25°C) of *Tetranychus urticae*.

Leaf number, counted from the top of a flowering rose shoot	n	Female *'egg-to-egg'* developmental (hours)		Net fecundity		Oviposition period (days)	
		$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$
2- 4th leaf	30	258	14	131.1	46.4	22.1	8.9
12-14th leaf	25	269	19	126.8	40.9	21.8	9.1
20-24th leaf	21	262	13	124.6	55.1	20.9	9.8

plant by the piercing of the leaf cells. Possibly the quality of available food dropped by indirect causes. Anyway, mite feeding activity does affect the food, as shown by a number of researchers (Davis, 1952; Bravenboer, 1959; Tulisalo, 1970; Rasmy, 1972; Wrensch & Young, 1975). To decide whether these factors need to be studied in more detail, a population experiment in the greenhouse was compared with population simulation, excluding density dependent factors (Part 2). In this way, if the simulations fit under circumstances of free growth (unlimited food supply), the critical level of plant exploitation may be found above which intraspecific competition acts upon the population growth of *Tetranychus urticae*.

2.1.3 Sex ratio

The two-spotted spider mite *Tetranychus urticae* is an arrhenotokous parthenogenetic species: unmated females produce only haploid eggs, which develop into males, whereas mated females produce both haploid and diploid eggs, which develop into males and females, respectively. Mating takes place immediately after the las moult of the female. Supply of sperm is organized very efficiently due to:

- the guarding and defending behaviour of the males (Potter et al., 1976a, 1978)
- the role of pheromones, tactile stimuli and web (Cone et al., 1971ab, 1972; Penman & Cone, 1972, 1974; Regev & Cone, 1975, 1976)
- a shorter developmental time of the males relative to the females (Subsection 2.1.1)
- a lower tendency of the males to disperse relative to that of the preoviposition females (Part 2)
- the presence of an overdose of males relative to the number of teleiochrysalids near the ecdysis (Potter, 1978; Functional sex ratio).

The insemination at the first mating appears to be the effective one (Helle, 1967; Overmeer, 1972; Wrensch & Young, 1978).

According to Boudreaux (1963) the proportion of females in the offspring of a single female is rather variable, so that there is no fixed sex ratio. He states, that the sex ratio in the offspring of each female depends on the amount of sperm received during mating. Though Overmeer (1972) demonstrated the possibility of such a relation by artificial *coitus* interruptions, it is still not clear if these interruptions occur under natural conditions. Moreover, Potter & Wrensch (1978) summarize some mechanisms that may lead to resistance of the males to disturbance by other males.

Although the sex ratio in the offspring of a single female is subject to variation, this need not to be true for the sex ratio in the offspring of a population of spider mites. Overmeer (1967) and Overmeer & Harrison (1969) found that the ratio of the total number of fertilized eggs against those that escape fertilization is rather fixed over a large number of subsequent opment with a Cahn electrobalance. The results (Table 12) are in close agreement with those of Mitchell (1973) and Thurling (1980), both obtained for *Tetranychus cinnabarinus*. The twenty-fold increase in weight, from egg to ovipositing female, takes place primarily in the deutonymph stage (30%) and the preoviposition stage (55%). This relative distribution of the weight over the developmental stages appears to be very similar to that of Phytoseiidae (Subsection 2.2.1, Table 18). Spider mites disperse to other leaves in the beginning of the preoviposition phase after fertilization. In this way colonizing females disperse before they have attained half their mature weight. By delaying half or more of their growth and their full reproduction effort until after dispersal to new food resources these mites reduce demands on their original location, where juveniles, males and parental females remain having a much lower tendency to disperse (Part 2).

The feeding physiology of spider mites is characterized by the large quantities of plant fluid passing the digestive system. McEnroe (1961, 1963), studying the actively feeding female by a radioactive tracer technique, estimated an ingestion rate equal to 6×10^{-3} µl per 30 minutes and a simultaneous defecation rate of 5×10^{-3} µl per 30 minutes. This implies that an amount of fluid equivalent to 20-25% of the female weight is passing the gut at 30 minute intervals. Liesering (1960) counted the number of parenchym cells punctured and emptied. His estimation of the ingestion rate amounts to 100 parenchym cells per 5 minutes, which, assuming the cell is spherical with radius 0.01 mm, implies an ingestion rat of 5 µl per hour. Elimination of the large quantities of water ingested in this way is accomplished via a bypass system that shunts excess fluids from the oesophagus directly into the hindgut. In this way ventricular digestion may proceed without the added burden of processing and transporting excess liquid (McEnroe, 1963). Large volumes of water can be passed rapidly through the digestive system and excreted without requiring energy for selective absorption and transport to the tracheal system for excretion. Also substances of low molecular weight (methylene blue solution) pass straight to the hindgut from the oesophagus. However a colloidal solution of Congo red is directed to the midgut (Akimov & Barbanova, 1978). Bekker (1956) supposed that chloroplasts and chlorophyll grains were phagocytized by disengaged epithelial cells, in which the stroma was being digested. Wiesmann (1968) showed that these free-living gut cells accumulated dyes, particles and especially chlorophyll, converting them ultimately into balls of excrement. Aggregations of these food balls in the U-shaped gut lumen have brought about the common name "two-spotted spider mite", due to the transparancy of the body wall. Upon excretion these so called "black pellets" contain a large amount of plant-pigment-related waste products (Blauvelt, 1945; Gasser, 1951; McEnroe, 1961; Liesering, 1960). Apart from these solid faeces another type of faeces can be distinguished. These are initially equal in size to the black pellets and spider mite eggs, but evaporate so quickly that only a very small solid fraction containing nitrogeneous waste products (McEnroe, 1961), remains: the "white pellets". Another means of eliminating large quantities of water is that via tracheal evaporation. By sealing the tracheal openings and by cyanide treatments, McEnroe (1961) showed that an important part of weight loss can be attributed to tracheal transpiration. Blauvelt (1945) showed the structural basis for the control of tracheal transpiration via the peritremes, which are located dorsally just behind the gnathosoma in this prostigmatid mite. The role of cuticular evaporation is very limited (McEnroe, 1961), probably because of a lipid layer in the cuticle (Gibbs & Morrison, 1959).

As expected of a plant-feeding arthropod, the conversion of ingested plant liquid into egg biomass is accomplished with low efficiency. A crude estimate of the conversion efficiency has been obtained from the following:

- The size of a fresh faecal pellet approximates that of an egg, so that their respective weights will not differ very much (approximately 1 µg) (own observation).
- The rate of oviposition is equal to 75% of the rate of defecation (relative humidity = 60-80%) (Hazan et al., 1973, 1975).
- The weight loss during the first hour of food deprivation is equal to 1.2 µg at T = 30°C and a relative humidity = 15-20% (McEnroe, 1961). This may be considered as an estimate of the tracheal transpiration rate.
- Oviposition and defecation at T = 30°C (and relative humidity = 15-20%) takes place at 2 and 1.5 hour intervals, respectively (Hazan et al., 1973, 1975), so that the weight loss via tracheal transpiration equals that via oviposition plus defecation.

The weight loss via oviposition therefore contributes to $3/7 \times 1/2$ = ca. 20% of the total weight loss. In the steady state (fluid intake = total weight loss), the conversion efficiency of ingested fluid to egg mass is equal to approximately 20%, which contrasts with that of the phytoseiid females (Section 3.1). Because mature females of this family lose most of their weight via egg production, Phytoseiidae can convert the ingested content of the spider mite to egg biomass with an efficiency of about 70%. This difference may be explained by a relatively higher degree of water conservation in the Phytoseiidae, as indicated by the presence of Malphighian tubules and a colon (Akimov & Starovir, 1975), and by a low proportion of indigestable constituents. In spider mites the physiological effort is not directed to recycling of water, but rather to eliminating it, as indicated by the presence of the combined hindgut and excretory organ (Blauvelt, 1945). Moreover, large amount of solid food residue are eliminated, as indicated by the "black pellets".

2.1.5 Role of webbing

Tetranychid species differ with respect to their mode of web formation. *Panonychus* spp. use the silken strands predominantly in dispersal (Fleschner et al., 1956). They spin threads by which they lower themselves from a leaf until they are picked up by air currents. Saito (1979) found that the females of *Panonychus citri* spin while walking, but appear to avoid their own threads, which merely serve as 'lifelines'. Apart from its similar use in dispersal, *Tetranychus* spp. use the silken strands as material for building structures of webbing, within which all stages find a place to live. The adult stages of these species walk upon, in or under the webs, while for example *Oligonychus ununguis* mostly lives under a webbing cover (Saito, 1979). The structure of these so called colonies differs among the members of the *Tetranychus* species. Colonies of *Tetranychus atlanticus* are more compact and have a greater profusion of webbing than those of most other species (Leigh, 1963). *Tetranychus desertorum* produces colonies similar to the latter species (Nickel, 1960), but *Tetranychus pacificus* produces only a loose or dispersed type of colony, with relatively little webbing. *Tetranychus urticae* produces colonies with an intermediate amount of webbing (Leigh, 1963). On the other hand the form and density of the web depends on the host plant involved (hairs, ribs, smoothness) (van de Vrie et al., 1972).

Several functions have been ascribed to the webbing (Gerson, 1979). The silk serves as ballooning threads in aerial dispersal, as a lifeline in dispersal by walking and as a carrier of sex pheromones. The webbing may indicate the state of depletion of food resources and it may be a prerequisite for the conditioning of social interactions. The webbing is used in intraspecific mating competition between males and in interspecific competition against other non-spinning phytophagous mites. The webbing cover may also exert an influence on the microclimate, for instance via the hygroscopic properties of the fibroin silk strands. Moreover, it protects the inhabitants from adverse climatic conditions, some pesticides and at least some natural enemies. In this study the effects of webbing on the acarine predator-prey interaction are considered. Not only because the webbing delimits the area occupied by the spider mites and therefore should be used in quantifying prey density, but also because it appears to be a very important cue in the foraging behaviour of the phytoseiid predators.

The role of webbing in the interaction between phytoseiid predators and tetranychid prey has been studied only a few times. McMurtry & Johnson (1966) state that *Amblyseius hibisci* sometimes backed away and proceeded in another direction when contacting the webbed area, whereas in other cases they walked over it, leaving the spider mites (*Oligonychus* spp.) unharmed. A few times this predator was observed inside the webbing structures having gained access to the prey. McMurtry & Johnson report that *Amblyseius limonicus* was less hindered by the webbing and *Amblyseius chilenensis* immediately crawled between the strands of webbing. A negative influence of webbing on predation by Phytoseiidae has been reported for the adult females of *Amblyseius longispinosus* (Mori, 1969), *A. largoensis* (Sandness & McMurtry, 1970, 1972), *Typhlodromus caudiglans* (Putman, 1962), *T. pyri* (McMurtry et al., 1970) and for the larvae of *T. tiliae* (Dosse, 1956); the adults of the latter species seemed not to be affected. However other Phytoseiidae seem to be attracted to the webbing and undisturbed by the silk. These include *Amblyseius fallacis*, *Phytoseiulus persimilis* and *Metaseiulus occidentalis* (Putman & Herne, 1966; Huffaker et al., 1969; McMurtry et al., 1970). Schmidt (1976) measured an increased rate of predation by *Phytoseiulus persimilis* due to the webbing. She found, that webs arrested the predator more than prey eggs or exuviae, and suggested, that this arrestment was based on tactile stimuli. These observations correspond with those of Takafuji & Chant (1976), who observed that *Phytoseiulus persimilis*, as opposed to *Iphiseius degenerans*, consistently distributed itself over the silk-covered leaves, and the adult females invariably deposited their eggs in the webbing. Fransz (1974, p. 99-100) concluded that webbing hinders *Metaseiulus occidentalis* sufficiently to affect the predation rate. He observed several behavioural changes of *Metaseiulus occidentalis* in response to webbing produced by the males of *Tetranychus urticae* (decrease of walking activity, walking velocity, coincidence of prey and predator and handling time with respect to the prey males). He stated that if this species is common in spider mite colonies, it is more due to the effect of trapping and a high reproduction rate in the presence of much food than by attraction. These findings stimulated the investigations discussed in this report on the role of webbing in the predator-prey interaction (Chapter 3).

2.1.6 Web production and colony growth

Tetranychus spp. produce silk strands (0.03-0.06 µm diameter) by way of a glandular system, which opens in a hollow hair at the top of the pedipalps (Mills, 1973; Alberti & Storch, 1974). The strands are stretched between the curved leaf edge, the leaf ribs and the leaf surface. When powdered with talc, the webbing becomes visible. It appears to be chaotically structured except that it tends to form a compact, coherent cover with a more-or-less obvious border. To quantify web production a fixed amount of fluorescent powder was dispersed over the webbed area, as proposed by Fransz (1974, p. 24). Some of the fluorescent particles stick to the silk strands, but the majority fall onto the leaf surface. The number of fluorescent particles stuck to the silk strands can be counted using a binocular microscope and a UV-lamp for illumination. These counts may serve as a relative measure of the amount of webbing, because they indicate the length of the silk strands. The webbing density is quantified by the number of intercepted particles per square centimetre of leaf area. To standardize the

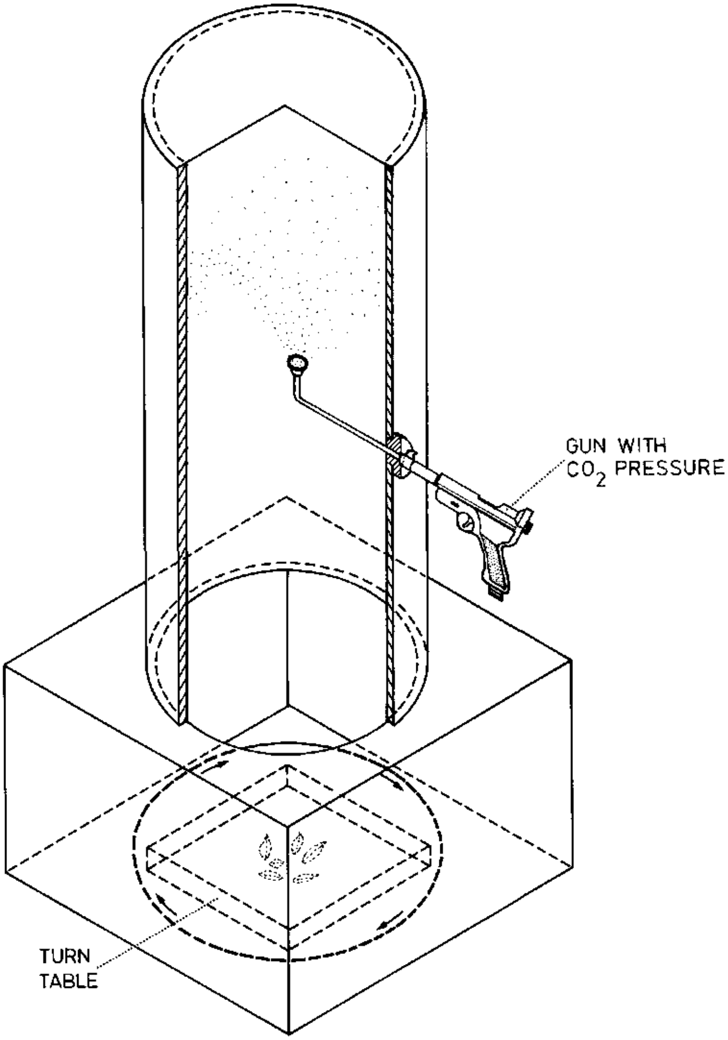


Fig. 7. Apparatus used for spraying fluorescent particles over the webbed rose leaves.

method of powder dispersal the following measures were taken:

- The fluorescent powder is kept in a desiccator to obtain particles of uniform size and prevent clotting.
- The amount of powder (1 mg) is accurately weighed on a Cahn electrobalance to obtain a number of particles subject to little variation.
- The particles are dispersed in an apparatus originally designed for fungal spore dispersal over a leaf area, aiming at a uniform distribution of the infection. The experimental design is given in Figure 7.
- All measurements are made simultaneously with a standard measurement of webbing, produced at T = 23°C and a relative humidity = 75%, to detect

variations in the experimental procedure and to enable correction for these variations if necessary.
These standard treatments were all within 15% of their overall mean, so that the experimental procedure was considered to be reliable.

Hazan et al. (1974) quantified the web production of *Tetranychus cinnabarinus* in a comparable way. They used the fraction of the total faecal-pellet production anchored to the silk threads as a measure for web production. Saito (1977a) developed a different approach to the problem. He constructed a grid of 1 mm mesh from thin (50 μm) nylon threads and placed it on the leaves. The mites produced webbing over the leaf-grid system. The mites were subsequently removed and the grid was lifted with the web threads attached. The amount of webbing was measured using dark-field microscopy. To date no comparison of these two methods has been reported in the literature.

The experiments on web production were carried out at three constant temperature levels (T = 15, 23, 29°C); the relative humidity was 75%. In another series of experiments measurements were made at three humidity levels (relative humidity = 45-50, 70-75 and 85-90%) and one constant temperature (T = 23°C). A Weiss Growth Cabinet (type ZK 2200 E/+4 JU-P-S), located at the Institute of Plant Protection Research, Wageningen, served as a climate room (T = x ± 0.25°C; relative humidity = y ± 2.5%).

Single preoviposition females were transferred to rose leaves that were still connected to a 5 cm section of their shoot. These females were allowed to produce eggs and web during a period equal to the mean incubation time of the eggs. Each experiment at a certain combination of T and RH was replicated at least 15 times. The results are given in Tables 13 and 14. These show that web production is stimulated by increasing temperature but is only slightly affected by changes in humidity within the range 50-85%. From

Table 13. Rate of increase of area webbed by *Tetranychus urticae*.

Temperature (°C)	Relative humidity (%)	Rate of increase of webbed area ($cm^2 \cdot day^{-1} \cdot ♀^{-1}$)		
		$\hat{\mu}$	$\hat{\sigma}$	n
13	70-75	0.016	0.005	20
16	70-75	0.057	0.014	16
23	45-50	0.167	0.039	21
23	70-75	0.157	0.046	18
23	85-90	0.129	0.043	19
29	70-75	0.218	0.032	12

Table 14. Web production of young females of *Tetranychus urticae*, as indicated by the interception of fluorescent particles.

Temperature (°C)	Relative humidity (%)	Rate of web production (particles·day^{-1}·♀$^{-1}$)		
		$\hat{\mu}$	$\hat{\sigma}$	n
13	70-75	8	3	20
16	70-75	26	8	16
23	45-50	72	14	21
23	70-75	63	11	18
23	85-90	54	9	19
29	70-75	102	19	12

the same experiments the daily expansion of the webbed area was measured. Since webbing became visible after powdering with fluorescents and UV-illumination, the circumference of the colony could be drawn on graphic paper. The rare case of a single strand stretched over a part of uncolonized leaf was neglected. As can be seen from Tables 13 and 14, the ratio of the daily increase of particle interception and that of the webbed area is about constant, so that apparently the web production is largely used for lateral expansion of the webbed area over the leaf surface. This does not mean that the webbing is distributed uniformly over the webbed area. The webbing density was mapped crudely and some characteristic cases are given in Figure 8. It appears that the lower densities are found in small strips near to the boundaries of the colony. However, to simplify further analysis it has been assumed that the webbing in a mite colony provides a homogeneous substrate for predator-prey interaction. This simplification must be kept in mind in interpreting results discussed in this report.

In a subsequent series of experiments the colonization period was not stopped after the elapse of the mean incubation time of the eggs, but the females and their offspring were allowed to continue feeding until the leaves were exhausted as a food source. In Figure 9 the change in webbing density is given for three characteristic sub-periods of spider-mite colonization of a leaf. In the first period only adult females produced webbing; the density of silk strands per square centimetre of webbed leaf area reached its maximum within a day of the transfer of females to the experimental leaf. In the second period the mite population consists of all possible stages of development. The webbing density increased only very slightly despite the increase in web-producing mites. This reflects a predominant lateral expansion of the colony. The third period started, when

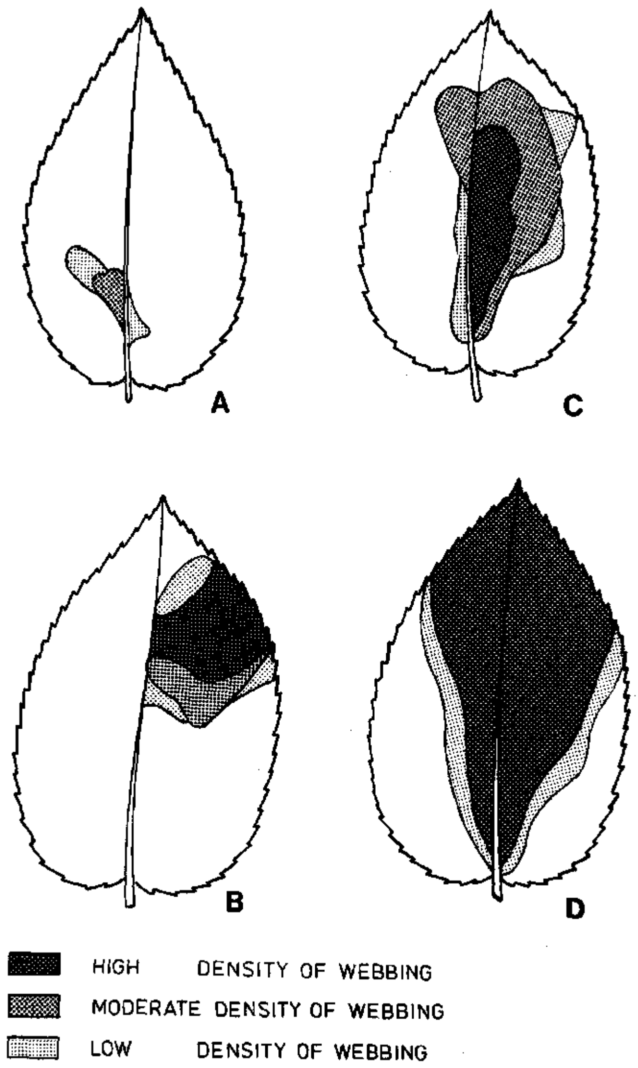


Fig. 8. Growth of the webbed area on the underside of a rose leaflet and a schematic representation of areas of high, moderate and low density of webbing. Leaf A until D represent increasing stages of colonization.

the food source was almost exhausted and the mites were becoming increasingly active, probably in search of food. There is an explosive increase in the amount of webbing due to the increase in walking activity. Saito (1977a) also noticed a high correlation between the walking activity and webbing. His observations clearly show that the spider mites continually produce threads while walking. Because silk secretion is probably not continuous, continuous thread production is probably due to the effect of silk coagulating by stretch.

rone (1968) showed that the Chilean population readily hybridizes with a Sicilian population, which is considered to be endemic (Ragusa, 1977). Many records from other Mediterranean countries are available (see e.g. McMurtry, 1977). This predator has been introduced in North American and European glasshouses to control spider-mite outbreaks. The results have been satisfactory (Hussey & Scopes, 1977).

Metaseiulus occidentalis (Nesbitt, 1951)

This species was obtained from the culture of Kuchlein (Agricultural University, Wageningen), which originated on the culture of Bravenboer (Glasshouse Crops Research & Experimental Station, Naaldwijk).

According to Hoying & Croft (1977) this population is conspecific with populations inhabiting citrus orchards in the western part of North America, where it is considered to be a successful predator of *Tetranychus mcdanieli* and, to a lesser extent, *Panonychus ulmi* (Hoyt & Caltagirone, 1971). The name of the genus (*Metaseiulus* instead of *Typhlodromus*) is adopted from Schuster & Pritchard (1963).

Amblyseius bibens Blommers, 1973

This species was obtained from the culture of van Zon & Blommers (Amsterdam, The Netherlands), where it was fed on *Tetranychus urticae*. Blommers (1973) collected specimens in Madagascar. He reports this predator to be successful in controlling *Tetranychus neocaledonicus* and *Tetranychus urticae* populations in the greenhouse (Blommers & van Etten, 1975; Blommers, 1976).

Amblyseius potentillae (Garman, 1958)

This species was obtained from the culture of van de Vrie (Wilhelminadorp, The Netherlands), where it was fed on *Tetranychus urticae*. The culture did not succeed on mite-infested bean plants, but was successful when mites were brushed off the leaves and offered to the predators (van de Vrie, personal communication; own observations).Van de Vrie collected specimens in the south-west part of The Netherlands (Serooskerke). Here it is considered to be an effective predator of *Panonychus ulmi*, together with other predatory mites like *Typhlodromus pyri* and *Amblyseius finlandicus* (van de Vrie, 1972; McMurtry & van de Vrie, 1973; Rabbinge, 1976). Boczek et al. (1970) recorded this species also in Central European orchards. Recently, McMurtry (1977) collected specimens in Southern Italy and showed that a stock from apple in The Netherlands was reproductively compatible with a stock from citrus in Italy (McMurtry et al., 1976).

The purpose of this study of phytoseiid predators is threefold:

- to analyse interspecific differences in development, abiotic mortality, fecundity and sex ratio in relation to temperature, humidity and prey den-

Table 10. Survey of the literature data concerning phytoseiid 'egg-to-egg' developmental time at different temperatures as compared with the results of the present work. Only proportional deviation (%) from own measurements are given. This deviation is defined as the difference between literature data on developmental time and own data divided by the latter data.

Species	Source	Temperature (°C)																					
			15					20					25					30					35
Phytoseiulus persimilis	Bravenboer & Dosse[a], 1962 (Table 1)		-10										-8					+0					+12
	Bravenboer & Dosse[a], 1962 (Figure 1)	-2					-15		+2	+9				+0		-13				+12	-11		
	Böhm[a], 1966			-3				+25					-8										
	Laing, 1968							+13															
	Begljarow, 1968					+2					+14				-4			+0					
	McClanahan, 1968							+4			-3			-17		-6							
	Takafuji & Chant,1976												+6										
	Fernando,1977							+25															
	Amano & Chant,1977										+3												
	Hamamura[a] et al.,1976a		-4					-1										-7					
	Stenseth[a], 1979		-3			-6			+29			+42			+60								
Metaseiulus occidentalis	Lee & Davis, 1968											-17											
	Laing, 1969							-9															
	Croft & McMurtry, 1972									-25													
	Pruszynski & Cone,1973					-25							-14					-12					+11
	Tanigoshi et al.,1976					+1			+6			+13			+17		+12			+5			+25
Amblyseius potentillae	Rabbinge, 1976		-18					+2					-15										
	McMurtry, 1977										+46												
Amblyseius bibens	Blommers, 1976			+22					+9			+5				+3		+1					

a. Time elapsed from egg to adult was used instead of from egg to egg!

sity (Subsection 2.2.1-2.2.3).

- to quantify the relative contribution of the different juvenile and adult stages of the predator to the prey consumption achieved in a whole life-span (Subsection 2.2.4).
- to estimate the effects of drinking water, cannibalism and, when tetranychid food is lacking, non-tetranychid food consumption on phytoseiid survival, and to determine their ability to recover from starvation (Subsections 2.2.5-2.2.7).

2.2.1 Development and mortality

Data on developmental time and mortality seem to be available (Table 16) in sufficient quantities. However many results are contradictory, which may be due to differences in strains or experimental methods, e.g. results of Bravenboer & Dosse on the developmental time of *Phytoseiulus persimilis* (Bravenboer & Dosse; Table 1 and Figure 1), results of Tanigoshi et al. (1977) and Pruszynski & Cone (1973) on the developmental time of *Metaseiulus occidentalis*, and results of McMurtry (1977) and Rabbinge (1976) on the developmental time of *Amblyseius potentillae*. Because of these differences interspecific comparisons were made simultaneuously between four phytoseiid species. This trial was carried out at three temperature levels (T = 15, 20, 30°C; relative humidity = 70%; photoperiod = 16 hours). At the start females were allowed to oviposit for two hours at T = 20°C. The eggs obtained in this way were immediately transported to the climatic cabinet. After hatching the larvae were put separately in Munger cages (Fig. 10), where they were supplied with abundant prey (eggs, larvae and females), throughout their development. The presence of exuviae was used as a criterium for previous moulting. The skins were discarded after detection. At the preoviposition phase of the females, two males were added per cage to ensure fertilization. The experiment was stopped after all females had deposited their first egg. In this way the progress in development was recorded every 8 hours with at least 30 replicates. The results are presented in Fig. 11 as the inverse of the time elapsed between egg sampling and the deposition of the first egg by the grown up female (the rate of 'egg-to-egg' development). The interspecific differences in the rate of development are summarized in linear equations relating the rate of development to the temperature (T = 15-30°C):

Phytoseiulus persimilis - rate = $0.011 \times (T-11.2)$ (day^{-1})
Amblyseius bibens - rate = $0.011 \times (T-11.5)$ (day^{-1})
Amblyseius potentillae - rate = $0.010 \times (T-11.0)$ (day^{-1})
Metaseiulus occidentalis - rate = $0.008 \times (T-11.0)$ (day^{-1})

Phytoseiulus persimilis develops somewhat faster than *Amblyseius bibens*, but much faster than *Metaseiulus occidentalis*. *Amblyseius potentillae* developed as fast as *Phytoseiulus*, but appeared to be better adapted to the lower

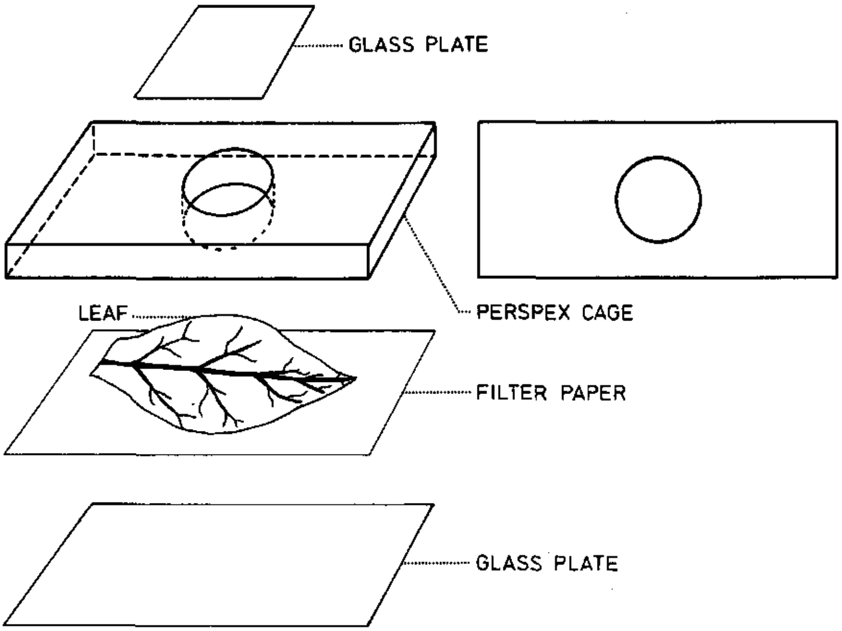


Fig. 10. Design of the Munger cage used in the study of *Phytoseiidae*.

temperature regime. This difference is possibly related to the climatic origin of these species. One common trait of the rate of development among the Phytoseiidae studied is that they develop faster than their prey: *Tetranychus urticae* - rate = 0.0067 × (T-11.0) (day^{-1}). Moulting causes only a very short interruption in the food searching activity of phytoseiids. Tetranychid development is characterized by distinct moulting stages of a duration similar to that of the preceding feeding stage. This causes an interruption of feeding and hence a retardation of development. From this point of view it is worthwhile to note that the egg-to-egg developmental periods of predator and prey equal each other, if the moulting stages are excluded from the computation of developmental time. The relative contribution of the hatching, intermoult and preoviposition periods to the total egg-to-egg period is about the same for all temperatures and for all species studied; on average 34% of the egg-to-egg period is spent in the egg stage, 12% in the larva stage, 15.5% in the protonymph stage, 16.5% in the deutonymph stage and 22% in the preoviposition stage (Table 17). The standard deviation and the mean of the developmental periods were estimated from a plot of the cumulative frequency distribution of developmental periods on probability paper of the Gaussian distribution. The 8-hour observation interval was taken as a class unit. The estimated standard deviations were 7-12% of the estimated mean developmental time. In Table 16 the proportional differences between the present measurements and those found in the litera-

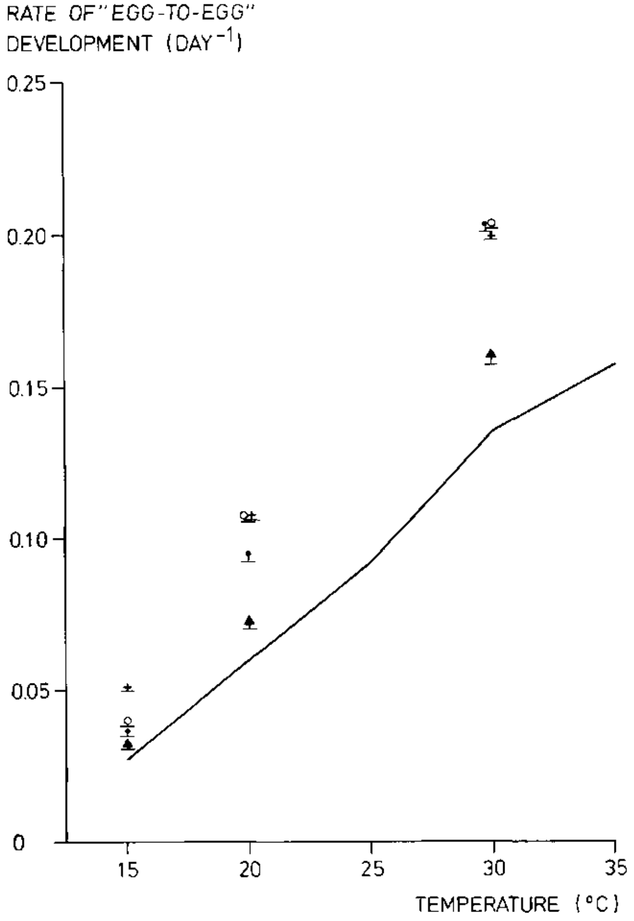


Fig. 11. Rate of egg-to-egg development of four phytoseiid species and the two-spotted spider mite in relation to temperature. o, *Phytoseiulus persimilis*; ●, *Amblyseius bibens*; +, *Amblyseius potentillae*; ▲, *Metaseiulus occidentalis*; ——— , the two-spotted spider mite, *Tetranychus urticae*; ⊥ , standard deviation (n = 30-50).

ture are summarized. Whenever the data in the literature concerned egg-to-adult periods instead of egg-to-egg periods, the length of the developmental period was adjusted accordingly. This survey demonstrates the large variation in the data from the literature compared to the data of this study. This may be due to strain specificness and/or experimental methods.

Even though the rate of development is related linearly to the temperature in the range of interest in this study, fluctuating temperatures may give rise to results that deviate from that expected for the linear relation. However Rabbinge (1976) showed that the rate of development may be considered as reacting instantaneously to a change in temperature (*Ambly-*

Table 17. Stage-specific developmental times of four phytoseiid species.

Species	Temperature (°C)	Mean developmental time (days)				
		egg	larva	proto-nymph	deuto-nymph	preoviposition female
Phytoseiulus persimilis	15	8.6	3.0	3.9	4.1	5.6
Amblyseius potentillae	15	6.8	2.4	3.3	3.4	4.2
Amblyseius bibens	15	9.2	3.2	4.3	4.5	5.8
Metaseiulus occidentalis	15	9.8	3.6	4.4	4.9	6.6
Phytoseiulus persimilis	20	3.1	1.1	1.4	1.6	1.9
Amblyseius potentillae	20	3.2	1.1	1.4	1.5	2.0
Amblyseius bibens	20	3.5	1.3	1.6	1.8	2.3
Metaseiulus occidentalis	20	4.4	1.7	2.0	2.4	3.1
Phytoseiulus persimilis	30	1.7	0.6	0.8	0.8	1.1
Amblyseius potentillae	30	1.6	0.7	0.8	0.8	1.1
Amblyseius bibens	30	1.7	0.7	0.8	0.8	1.1
Metaseiulus occidentalis	30	1.7	0.8	0.9	1.0	1.3

seius potentillae).

Begljarow (1967), Ushekov & Begljarow (1968) and Stenseth (1979) showed that developmental time is also affected by relative humidity. Only a slight increase in developmental time was observed by these authors when the relative humidity was increased from 40% to 70%. The tendency to gain water by increased predation at low humidity may account for this reduced effect (Begljarow, 1967; Pruszynski, 1977). According to Begljarow, development almost stops at relative humidities of 25-35%.

In the present experiments, mortality during development was as low as in *Tetranychus urticae*. At all temperatures 87-94% of the eggs reached maturity, independent of the species involved (RRM = -ln(0.9) × DR; RRM = relative rate of mortality; DR = 'egg-to-egg developmental rate). In another experiment the effect of extreme temperatures was investigated for *Phytoseiulus persimilis* and *Metaseiulus occidentalis*; a five-day period of the eggs at T = 10°C did not alter the percentage of eggs reaching maturity in a subsequent period at T = 20°C and relative humidity = 70%. At T = 35°C and relative humidity = 75% the pre-adult mortality rose to 24%. According to Hamamura et al. (1978) the eggs of *Phytoseiulus persimilis* failed to hatch after storage periods of more than 6 days at temperatures below 10°C, but the adult females were able to survive and to remain reproductive after 25 day storage without food, after 50 day storage with honey and after 70 day storage with spider mites, when relative humidity was sufficiently high.

According to Begljarow (1967) the mortality in the egg stage depends very much on the humidity level. At a relative humidity of 50% the eggs of *Phytoseiulus* appeared to shrivel at all temperatures between 13°C and 37°C. At a relative humidity of 60% hatching of the eggs was successful below T = 30°C, but above this temperature level a relative humidity of 80% was necessary for successful hatching. Larvae, nymphs and adults were less affected by humidity, probably due to a compensatory moisture supply through increased predation at decreasing humidities. They could develop normally at relative humidity = 50%, but at 25-35% stopped (Begljarow, 1967). A number of authors confirmed the fact that the egg stage of *Phytoseiulus persimilis* is relatively vulnerable to relative humidities below 70% (Ushekov et al., 1968; Hamamura et al., 1978; Pralavorio et al., 1979; Stenseth, 1979). A similar type of vulnerability was found by McMurtry et al. (1976) for *Amblyseius potentillae*. An Italian stock of this species appeared to be more resistant to low humidities than a Dutch stock (50% mortality of the eggs at relative humidities of approximately 55% and 70%, for the respective stocks). McMurtry et al. state that these results are consistent with the climatic origin of the stocks and that the egg stage is probably the most vulnerable to dry conditions: the mobile stages can obtain moisture from their food or move to a more favourable (micro)climate. However, although the egg itself is immobile, it is deposited by the adult female predator at characteristic spots on the leaf (e.g. stuck to the leaf hairs), often close to the leaf ribs and - most important with regard to the Phytoseiidae in question - in the webbing structure produced by their prey. As postulated by Hazan et al. (1975), the hygroscopic properties of the fibroin silk strands, the microclimate in the webbing structure, the supply of moisture via evapotranspiration of the leaf and, to a smaller extent, defecation by the spider mite may buffer the low humidity levels in the plant environment.

Because the greenhouse climate is such that relative humidities between 40% and 70% do occur rather frequently, the extent to which the microhabitat buffers the effect of humidity was investigated. Two substrates for egg development were placed simultaneously in a controlled-environment room:

- plant with webbing and mites (eggs and adults) (Fig. 12);
- uncovered Munger cage without leaves, webbing and spider mites (= Perspex substrate).

Subsequently, well-fed female predators were released on these substrates

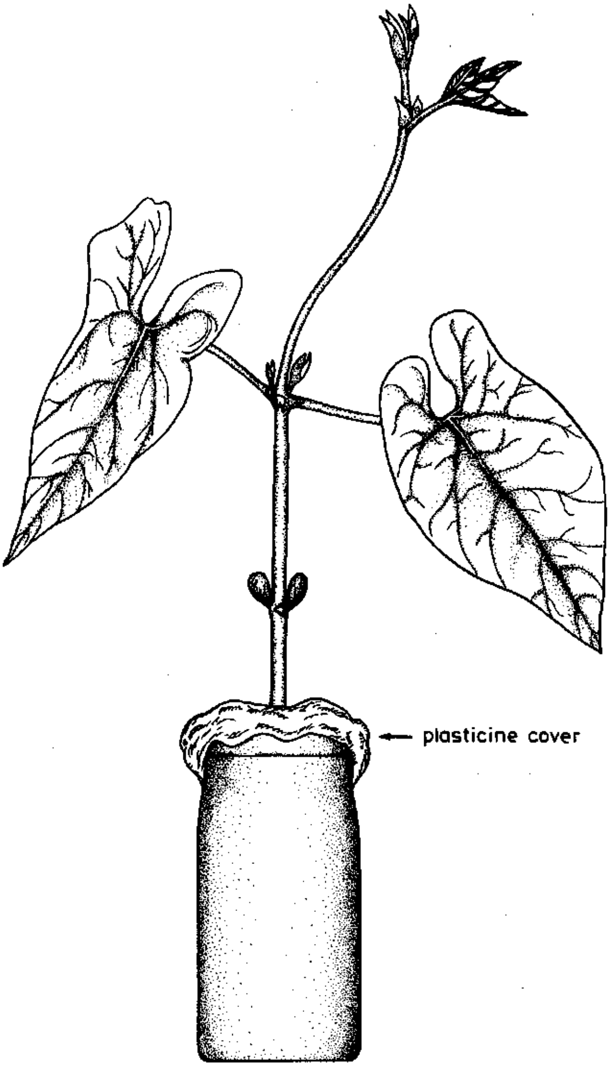


Fig. 12. Plant system used in the study of climatic effects on life history.

and were allowed to oviposit for one day. In this way, the eggs were not deposited in an artificial way, but according to the oviposition behaviour of the female predator. After removal of the ovipositing females the hatching success of the predator eggs was recorded during the following six days. The results (Fig. 13) show that in comparison with the artificial substrate the combination of plant, webbing and spider mites exerts a positive influence on the hatching success. Under the climatic regime of the greenhouse culture of ornamental roses (relative humidity > 50%) no detrimental effects are to be expected because the hatching success declines for relative humidities below 50%, even at high temperatures. The results concerning the artificial substrate correspond with reports of similar investigations (Ushekov

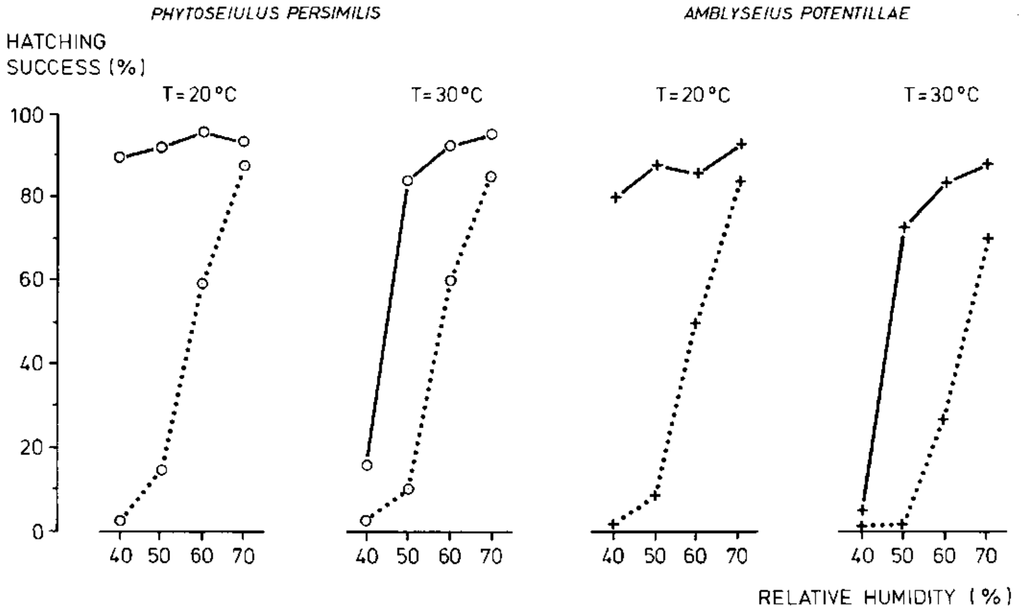


Fig. 13. Hatching success of the eggs of two phytoseiid species (o = *Phytoseiulus persimilis* and + = *Amblyseius potentillae*) in relation to relative humidity and to the substrate. ——, webbed bean leaves (Fig. 12); ····, uncovered Munger cages (Fig. 10).

et al., 1968; Pruszynski, 1977; Pralavorio et al., 1979; McMurtry, 1977). Those concerning the 'natural' substrate correspond with the results of Stenseth (1979), who used the appropriate experimental procedure at two extreme humidities (relative humidity = 80% and 40%).

The reports of juvenile mortality at high temperatures (T > 30°C) are numerous. Bravenboer & Dosse (1962) did not report an increase in mortality of *Phytoseiulus* juveniles at T = 30°C and 35°C; Hamamura et al. (1976a) found a high mortality of *Phytoseiulus persimilis* at temperatures *above* 30°C; Begljarow (1968) and Böhm (1970) observed low viability of the eggs at temperatures *above* 30°C and McClanahan (1968) found a very high mortality even *at* T = 30°C. Similarly for *Metaseiulus occidentalis*, there are reports of increasing mortality above 33°C (Pruszynski & Cone 1973, high mortality at T = 35°C; Tanigoshi et al. 1975, 100% mortality at T = 38.4°C). The interpretation of these results is very difficult, both through lack of specification of the environmental humidity and lack of uniformity in the experimental substrates. The experiments described in this study did not indicate an increase in mortality at T = 30°C and high humidity, but the critical humidity level, below which mortality increases, is raised by increasing temperatures (see Begljarow, 1968). Probably the rapid onset of detrimental effects cannot be prevented by high humidities when temperature

Table 18. Stage-specific fresh weights (μg) of four phytoseiid species.

Predator species	Egg[a]	Larva[b]	Proto-nymph[b]	Deuto-nymph[b] ♀	Male[b]	Female[a]
Phytoseiulus persimilis	4.5-4.8	4.0-4.8	5.2-6.7	9.7-10.9	5.4-6.7	24.1-28.9
Amblyseius potentillae	2.9-3.3	-	-	-	-	15.1-17.9
Amblyseius bibens	2.0-2.4	-	-	-	-	10.1-12.2
Metaseiulus occidentalis	1.8-2.1	1.8-2.2	2.3-2.9	3.1-3.9	2.5-3.0	8.0-10.4

a. Number of replicates = 20.

b. Number of replicates = 5.

exceeds 32°C.

Measurements of the weight increase during development are given in Table 18. The males attain their final weight level in an early stage of development: the protonymph stage. The females obtain almost 60% of their weight increase during the preoviposition period. The maximum difference in weight between females sampled from well-fed cultures at or before oviposition almost corresponds with the weight of an egg. This is because one egg at a time (= the terminal oöcyte) is absorbing vitellogenic materials. After attaining its final size and fertilization the egg will be deposited and the next egg in the 'queue' will start growing. The adult ovipositing female weighs 4-5 times more than the original egg mass, a ratio that holds for all species studied. Furthermore, it appears that though the relative weight increase is constant for the species studied, absolute weight levels differ considerably. As shown in Fig. 3, *Metaseiulus occidentalis* is the smallest phytoseiid of the four studied. Relative to this species the ovipositing females of *Phytoseiulus persimilis* contain 2-3 times more biomass, *Amblyseius potentillae* 1.5-2 times more and *Amblyseius bibens* 1.1-1.3 times more.

The effect of food supply on the rate of development is demonstrated in Table 19, which presents some unpublished data of Kuchlein and data from the literature (van de Vrie, 1973; Takafuji & Chant, 1976). The critical level of food supply, below which development is retarded and mortality increases, is about 1-2 μg per day. From the interspecific and stage-specific weight distributions, it is obvious that the effects are more pronounced in the larger-sized phytoseiid species and in the preoviposition phase, in which relative to the other stages a large weight increase has to occur in a short time span. The larvae of all species in question are able to moult

Table 19A. The influence of the density of the prey on the developmental time of *Metaseiulus occidentalis*. Leaf area = 5 cm^2; daily replacement of the prey consumed; T = 27°C. Source: Kuchlein (to be published).

Prey (eggs) number	Developmental time (days)								
	egg	n	larva	n	protonymph	n	deutonymph	n	egg to adult
1	1.7	44	1.16	37	1.94	32	1.26	27	6.06
2	1.72	69	0.98	65	1.26	57	1.02	51	4.98
4	-	-	0.97	76	1.00	73	1.00	73	4.67
25	1.61	74	1.01	69	1.01	67	0.93	67	4.56
50	1.81	99	0.90	90	0.89	82	0.95	75	4.55

Table 19B. The influence of prey density on the developmental time of *Phytoseiulus persimilis*. n = 10-14; paper area = 4 cm^2; daily replacement of the prey consumed; T = 25°C. Source: Takafuji & Chant (1976).

Prey (protonymphs) number	Developmental time (days)			
	larva	protonymph	deutonymph	egg to adult
1	0.8	2.8	5.1	8.7
2	0.8	1.2	1.7	3.7
4	0.8	1.2	1.2	3.2
20	0.8	1.2	1.2	3.2
Prey (adult ♀) number	**Preoviposition**			
1	5.5			
2	4.1			
4	2.9			
8	2.0			
16	1.5			
32	1.4			

into the next nymphal stage without any food and without any retardation of development, but moulting from the first to the second nymphal stage does require food consumption. When prey eggs are in abundance *Phytoseiulus persimilis* and *Metaseiulus occidentalis* consume 15 and 8 eggs, respectively,

Table 19C. The influence of prey density on the developmental time (days) of *Amblyseius potentillae*. n = 11-13; cage area = approx. 20 cm^2; daily replacement of the prey consumed; T = 23°C. Source: van de Vrie (1973).

Prey (larvae) number	Developmental period (egg to adult)	Preoviposition period
high	6 (5-6.5)	2 (1.5- 3.5)
10	6 (5-6.5)	2 (1.5- 3.5)
4	8 (7-9.5)	4 (3.5- 5.5)
2	12 (10-18)	8 (7.0-10.5)

during nymphal development (Subsection 2.2.4). These quantities of food required are constant at all temperatures, which suggests a fixed amount of food needed to mature. However, phytoseiids are able to mature on 66% of the food quantity described previously (own observation). Although their bodies were flattened under conditions of low food supply, they were still able to moult into the next stage despite their obviously hungry state. Apparently development allows for some flexibility with respect to the food requirements in the nymphal stages.

2.2.2 Sex ratio

For four phytoseiids, egg production commences only after copulation (McMurtry et al., 1970; Schulten et al., 1978; personal observation). Although karyological evidence indicates that males are haploid and females diploid (Wysoki & Swirski, 1968; Blommers & Blommers-Schlösser, 1975; Oliver, 1977), both males and females probably result from diploid eggs, as has been shown by genetic means for the case of *Amblyseius bibens*, *Phytoseiulus persimilis* (Helle, 1978) and *Metaseiulus occidentalis* (Hoy, 1979). Apparently the haploid condition of the males is caused by the loss and/or heterochromatization of half of the chromosomes. Thus parahaploidy, not arrhenotoky, as found in the spider mites, is the genetic system (Hoy, 1979).

The probability that an egg becomes a male or a female can be estimated from the sex ratio (♀/(♀ + ♂) in a large sample taken from eggs lain by randomly selected phytoseiid parents. Sex distinction is most conveniently made in the adult phase: females are larger than males. The proportion of females can thus be assessed in the group of adults emerging from a laboratory *ab ovo* cultivation. This proportion equals the sex ratio if the relative rate of juvenile mortality of both sexes are the same. In Table 20 a data survey is given for 'laboratory' sex ratios of the four Phytoseiidae. Although the sample size of the parental females is generally small, it

Table 20. Sex ratio in the progeny of four phytoseiid species according to references in the literature.

Predator species	Temperature (°C)	Sex ratio ♀/(♀ + ♂)	Number of eggs	Number of parental females	Reference
Phytoseiulus persimilis	23	0.89	954	-	Amano & Chant, 1978
	25	0.86	816	11	Schulten et al., 1978
	25	0.84	930	13	Hamamura et al., 1976a
	25	0.82	400	100	Takafuji & Chant, 1976
	15-28	0.804	245	20	Laing, 1968
	22-27	0.79	247	20	Kennett et al., 1968
Metaseiulus occidentalis	18	0.66	-	50	Tanigoshi et al., 1977
	21	0.70	-	50	Tanigoshi et al., 1977
	24	0.64	-	50	Tanigoshi et al., 1977
	27	0.68	-	50	Tanigoshi et al., 1977
	29	0.68	-	50	Tanigoshi et al., 1977
	32	0.62	-	50	Tanigoshi et al., 1977
	35	0.60	-	50	Tanigoshi et al., 1977
	24	0.53	43	-	Lee & Davis, 1968
	22.5	0.63	620	60	Croft & McMurtry, 1972
	22.5	0.55	179	20	Croft & McMurtry, 1972
	15-28	0.71	-	-	Laing, 1969
	25.5	0.62	-	-	Sharma[a], 1966
Amblyseius bibens	29	0.83	360	54	Blommers, 1976
Amblyseius potentillae	15-30	0.69	238	85	Rabbinge, 1976

a. Ph.D. thesis, referred to in Croft & McMurtry (1972).

seems justified to conclude that for all four species the sex ratio generally exceeds 50% and that there are interspecific differences. The sex ratios of *Amblyseius potentillae* and *Metaseiulus occidentalis* are around 66%, while those of *Phytoseiulus persimilis* and *Amblyseius bibens* are close to 83%.

Based on both laboratory sex ratios and sex ratios observed in the field, the sex ratio may be considered constant, although a few exceptions are noteworthy:

- Tanigoshi et al. (1977) established a slight decrease of the sex ratio of *Metaseiulus occidentalis* at temperatures exceeding 30°C.
- Dyer & Swift (1979) found that short-term variations in sex ratio were related to meteorological changes, particularly humidity, temperature and wind speed. The reason is not yet clear.
- Amano & Chant (1978) observed that the sex ratio of *Phytoseiulus persimilis* was constant with age, except for a higher proportion of male progeny at the onset of reproduction.
- Amano & Chant (1978) found that the sex ratio was independent of the feeding history of the female as a juvenile, but in comparison with well-fed females temporary food deprivation in the adult stage gave rise to a decrease of the sex ratio in the subsequent offspring.

The causes of the deviating 'laboratory' sex ratios may be due to both differences in mortality among the sexes and the sex determination process. The 'field' sex ratios are also influenced by the shorter life span of the males, differential susceptibility to detrimental factors, etc.

There seems to be no reason why adult females should not mate shortly after emergence:

- The eggs are deposited in prey aggregations, so that emerging males and females are in close vicinity.
- The tendency to disperse is low in all stages relative to that in the fertilized females (Section 3.4). The food requirements for development are very low and even flexible to a certain extent (see Subsection 2.2.1), so that the aggregation of the juvenile, male and virgin female phytoseiids has no severe effect on prey availability and when prey becomes scarce, the strongest individuals can survive and develop by way of cannibalism (Subsection 2.2.6).
- The sex-attracting cues are probably only effective over short distances (Rock et al., 1976; Hoy & Smilanick, 1979) and the proportion of males in the offspring is always less than 50%.
- Severe starvation is not detrimental to the willingness to mate (Ragusa & Swirski, 1977; Blommers et al., 1979).

A single mating is sufficient to achieve maximal fecundity in the case of *Phytoseiulus persimilis* (Schulten et al., 1978; Amano & Chant, 1978). However Hamamura et al. (1976a) found, that those females that had deposited less than 43 eggs, restarted to oviposit after the reintroduction of a male on day 33 since first oviposition. Surprisingly the sex ratio of the 'second'

Table 21. Survey of the literature on fecundity (number of eggs) and on life-span of some phytoseiid predators.

Species	Temperature (°C)	Potential fecundity	Net fecundity				Reference
		$\hat{\mu}$	$\hat{\mu}$	$\hat{\sigma}$	n	range	
Phytoseiulus persimilis	-	-	81.2	-	-	-105	Begljarow & Hlopceva, 1965 (A)
	-	-	75.0	-	-	- 87	
	-	-	51.8	-	-	- 63	
	15-28	73.2	53.5	-	38	14-101	Laing, 1968 (B)
	20	-	43.8	23.3	10	- 78	McClanahan, 1968 (C)
	26	-	53.5	20.7	12	- 87	
	-	-	62.0	-	-	-	Kamath, 1968 (D)
	25-26	-	59.0	-	-	-	Böhm, 1966 (E)
	22-27	-	56.1	-	20	-	Kennett & Caltagirone, 1968 (F)
	22-27	-	64.7	-	20	-	
	-	-	74.5	-	-	-	Plotnikov & Sadkowskij, 1972 (G)
	23	-	71.9	15.3	10	-	Amano & Chant, 1977 (H)
	25	-	79.5	25.2	30	-	Takafuji & Chant, 1976 (I)
	25	-	71.5	20.4	13	23-93	Hamamura et al., 1976a (J)
	17	-	65.5	-	12	51-79	Pruszynski, 1977 (K)
	21	-	73.1	-	12	60-85	
	26	-	74.1	-	12	66-87	
	-	-	78.0	-	18	52-93	
	-	-	70.9	-	19	42-91	(eggs as food)
	-	-	57.9	-	12	36-89	(larvae as food)
	25	-	74.2	-	11	59-98	Schulten et al., 1978 (L)
	20	-	78.8	19.2	16	12-95	Fernando, 1977 (M)
	5	-	0	-	14	-	Pralavorio, 1979 (N)
	5-12	-	16.8	-	21	-	
	10	-	31.0	-	25	-	
	20	-	80.2	-	24	-	
	30	-	16.4	-	25	-	
Amblyseius potentillae	10	-	9.0	-	10	-	Rabbinge, 1976 (O)
	15	-	20.0	-	10	-	
	20	40.9	27.8	-	38	-	
	25	-	29.1	-	9	-	
	30	23.3	16.0	-	38	-	
Amblyseius bibens	22	65.0	63.2	-	54	-	Blommers, 1976 (P)
	25	64.1	60.1	-	54	-	
	29	63.7	63.6	-	54	-	
	29	-	39.5	-	20	30-49	Schulten et al.[a], 1978 (Q)
Metaseiulus occidentalis	24	-	33.7	-	51	21-56	Lee & Davis, 1968 (R)
	15-28	41.8	34.0	-	25	14-53	Laing, 1969 (S)
	22.5	-	33.8	-	80	-	Croft & McMurtry, 1972 (T)
	24	-	37	-	30	-	Croft, 1972 (U)
	18.5	-	33.8	-	10	13-55	Pruszynski & Cone, 1973 (V)
	25	-	35.2	-	12	21-54	
	30	-	28.2	-	12	17-48	
	18	-	21.9	-	50	-	Tanigoshi et al., 1976 (W)
	21	-	28.1	-	50	-	
	24	-	29.6	-	50	-	
	27	-	33.1	-	50	-	
	29	-	28.2	-	50	-	
	32	-	33.4	-	50	-	
	35	-	27.8	-	50	-	
	27	50.0	44.0	-	54	-	Kuchlein (to be published) (X)

a. Females had mated only once.

Table 21. Continued.

Ref.	Preoviposition period				Oviposition period				Postoviposition period				Female longevity			
	$\hat{\mu}$	$\hat{\sigma}$	n	range	$\hat{\mu}$	$\hat{\sigma}$	n	range	$\hat{\mu}$	$\hat{\sigma}$	n	range	$\hat{\mu}$	$\hat{\sigma}$	n	range
A	-	-	-	-	-	-	-	-	-	-	-	-	22	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	19	-	-	-
B	3.0	0.6	22	2.2-4.2	22.3	-	38	6-39	7.3	-	38	-	32.6	-	38	12- 50
C	-	-	-	-	-	-	-	- 31	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	- 17	-	-	-	-	-	-	-	-
D	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F	-	-	-	-	15.1	-	20	-	-	-	-	-	-	-	-	-
	-	-	-	-	18.6	-	20	-	-	-	-	-	-	-	-	-
G	-	-	-	-	±21	-	-	-	-	-	-	-	-	-	-	-
H	1.3	0.3	16	-	23.3	5.5	10	-	0.7	0.8	10	-	25.1	5.7	10	-
I	1.5	0.5	30	-	21.6	6.0	30	-	13.1	7.7	30	-	36.2	9.3	30	-
J	1.3	-	-	-	17.2	4.8	13	-	-	-	-	-	49.0	11.1	13	-
K	-	-	-	-	33.6	-	12	26-38	-	-	-	-	56.3	-	12	23- 92
	-	-	-	-	26.3	-	12	22-37	-	-	-	-	54.1	-	12	19- 93
	-	-	-	-	18.8	-	12	16-23	-	-	-	-	38.2	-	12	15- 58
	-	-	-	-	33.8	-	18	25-48	-	-	-	-	77.9	-	18	49-123
	-	-	-	-	24.3	-	19	13-33	-	-	-	-	51.1	-	19	15-138
	-	-	-	-	23.1	-	12	12-36	-	-	-	-	37.5	-	12	19-128
L	-	-	-	-	10-15	-	-	-	-	-	-	-	-	-	-	-
M	3.3	0.4	15	2.9-4.5	37.1	8.8	16	6-44	22.7	11.3	11	6-44	50.9	17.0	19	10- 72
N	-	-	-	-	-	-	-	-	-	-	-	-	52	-	14	-
	-	-	-	-	43	-	-	-	-	-	-	-	65	-	21	-
	-	-	-	-	44	-	25	-	-	-	-	-	68	-	25	-
	-	-	-	-	30	-	24	-	-	-	-	-	45	-	24	-
	-	-	-	-	5.5	-	25	-	-	-	-	-	9	-	25	-
O	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	7.4	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	4.0	1.0	-	-	22.2	11.8	35	4-41	8.0	9.1	35	0-28	34.2	-	35	-
	1.9	0.9	-	-	15.1	8.5	8	6-28	7.6	8.4	8	0-28	24.6	-	8	-
	2.9	0.8	-	-	13.4	7.8	37	2-44	10.8	11.0	37	0-45	27.1	-	37	-
P	-	-	-	-	-	-	-	- 46	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	- 28	-	-	-	-	-	-	-	-
	1.2	-	-	-	-	-	-	- 23	-	-	-	-	-	-	-	-
Q	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R	1.3	-	51	1-2	-	-	-	-	-	-	-	-	38.7	-	51	21-56
S	3.2	0.4	18	2.5-4.0	15.9	± 2	25	7-25	1	-	-	-	20.2	6.2	18	10-30
T	1.5	-	-	-	-	-	80	27-41	-	-	-	-	-	-	-	-
U	-	-	-	-	-	-	30	16-29	-	-	-	-	-	-	-	-
V	2.8	-	10	2-3	27.1	-	10	15-39	-	-	-	-	-	-	-	-
	1.2	-	12	1-1.5	14.3	-	12	10-18	-	-	-	-	-	-	-	-
	1	-	12	0.8-1.3	10.9	-	12	7-15	-	-	-	-	-	-	-	-
W	4.1	-	50	-	17.6	-	50	-	-	-	-	-	-	-	-	-
	2.7	-	50	-	16.0	-	50	-	-	-	-	-	-	-	-	-
	2.4	-	50	-	13.9	-	50	-	-	-	-	-	-	-	-	-
	2.4	-	50	-	13.4	-	50	-	-	-	-	-	-	-	-	-
	1.3	-	50	-	11.5	-	50	-	-	-	-	-	-	-	-	-
	1.1	-	50	-	11.4	-	50	-	-	-	-	-	-	-	-	-
	1.5	-	50	-	9.5	-	50	-	-	-	-	-	-	-	-	-
X	1-2	-	-	-	-	-	-	-	-	-	-	-	27.1	13.8	67	3-60

brood had decreased to 76%. *Amblyseius bibens* (Schulten et al., 1978), *Metaseiulus occidentalis* (Kuchlein, personal communication) and *Amblyseius potentillae* deposit only about 2/3 of their total egg potential for only one mating. Hence more than one mating is required to maximize reproduction.

2.2.3 Adult life span and fecundity

From the literature data in Table 21 on phytoseiid longevity and fecundity at various temperatures and high prey density, it follows that:

- Interspecific differences in female longevity are absent, but the species-specific fecundities decrease in the following order: *Phytoseiulus persimilis* (approx. 70), *Amblyseius bibens* (approx. 60), *Metaseiulus occidentalis* (approx. 35), *Amblyseius potentillae* (approx. 30).
- Strain specific fecundities may be present, as indicated by the differences between the Dutch strain of *Phytoseiulus persimilis* (Pruszynski, 1977; Schulten et al., 1978) and the others. A similar indication can be found by comparison of the data of Kuchlein and the North American reports for *Metaseiulus occidentalis*.
- Net fecundity is 70-97% of the potential fecundity (female mortality excluded).
- The oviposition period is shortened by increasing temperatures. Female longevity is less affected as the postoviposition period is rather variable.
- Fecundity is probably maximal in the temperature range of 17-28°C. Only a few data are available at temperatures below 17°C, but a decrease is expected. At temperatures above 28°C such a decrease will eventually occur also, but the critical temperature is not known.

To complete these results interspecific comparisons at low (12 and 15°C) and high (30 and 33°C) temperatures are necessary. These reproduction experiments were carried out in Munger cages with ample supply of prey (eggs and larvae) and high relative humidity (relative humidity = 85%). At the start a young fertilized female and two males were put into each cage and subsequently the number of eggs deposited was recorded daily. The results (Table 22) indicate that except for *Amblyseius potentillae* the critical upper limit is above 33°C. In the latter case the limit is somewhere between 25 and 30°C. On the other hand, when considered relative to their maximal fecundity the decrease in fecundity below 17°C was almost equal among the species.

Several authors have established a decrease in the rate of reproduction at humidities below 65% (Ustchekow et al., 1968; Begljarow, 1968; Pruszynski, 1977; Pralavorio, 1979). However these data were not derived from experiments on intact plants, so that the effect of the humidity buffering capacity of the plant was not included in the assessment of the critical humidity level. Relative humidity is critical below 50%, as experiments on the sensi-

Table 22. Net fecundity (number of eggs) of four phytoseiid species at some extreme temperatures.

Species	T = 12°C			T = 15°C			T = 30°C			T = 33°C		
	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n
Phytoseiulus persimilis	20.2	7.2	15	40.9	15.2	25	62.8	19.2	25	60.8	14.3	25
Amblyseius bibens	13.4	5.2	20	48.2	16.4	20	60.8	16.3	20	58.8	14.1	20
Metaseiulus occidentalis	9.4	2.8	20	30.1	12.4	18	41.3	11.0	20	44.0	12.7	20
Amblyseius potentillae	10.2	3.3	15	22.5	9.8	15	21.4	13.2	25	16.5	7.7	25

tivity of hatching success to humidity indicate. Therefore it is assumed that no detrimental effects of humidity are to be expected under the climatic regime occurring for the greenhouse culture of ornamental roses.

The rate of food conversion into egg biomass is very high. Ovipositing phytoseiid females have a daily egg biomass production equal to half their maximum body weight, which is taken to be their mean weight just prior to egg laying. Moreover, although the fecundity of phytoseiids is 2-4 times lower than that of the spider mites, the biomass of eggs produced may be equal (*Amblyseius bibens*) or even two times larger (*Phytoseiulus persimilis*). Because of the high production of egg biomass the supply of prey will be very important to these predators in realizing their reproductive potential. The effect of prey egg density on the life span and net fecundity of *Metaseiulus occidentalis* is given in Table 23 and Fig. 14. The mean life span is double at a prey density of 1-2 eggs per 5 cm^2 leaf disc, replacing the prey eaten by the predator or died from other causes at daily intervals. The cumulative number of eggs produced per living female is plotted against time elapsed since the last moult of the female for various levels of the prey density. The ultimate number of eggs produced (= potential fecundity) decreased from 74% at 4 prey eggs per 5 cm^2 to 44% at 2 prey eggs per 5 cm^2 and next to 10% at 1 prey egg per 5 cm^2.

The rate of reproduction does not depend on the age of the female, but rather on the number of eggs already deposited:

- Virgin females retain the ability to produce eggs all their life. Their age at fertilization does not influence the subsequent rate of reproduction nor the sex ratio (Schulten et al., 1978).
- Adult female Phytoseiidae retain their ability to produce a normal egg number after any period of food deprivation, unless prevented by death or old age (> 50 days). See Table 24 and Blommers et al. (1979). Ashihara et

Table 23. The influence of prey density on female longevity of *Metaseiulus occidentalis*. T = 27°C; relative humidity = 60-80%; daily replenishment of the prey consumed. Source: Kuchlein (to be published).

Prey (egg) density	Life-span (days)		
(number/5 cm^2)	$\hat{\mu}$	$\hat{\sigma}$	n
0			
1- 2	56.8	27.1	19
4- 10	41.1	13.1	37
25- 50	26.8	13.7	51
75-150	27.5	14.0	16

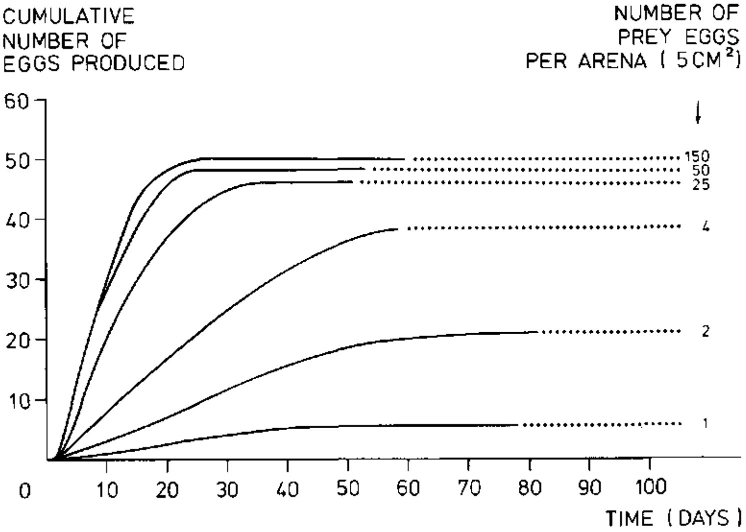


Fig. 14. Influence of prey egg density on the potential fecundity of *Metaseiulus occidentalis*. (Data from Kuchlein, to be published)

al. (1978) similarly found, that the reproductive potential of females of *Phytoseiulus persimilis* had been maintained after being reared for 35 days on a diet of honey.

- Reproduction stops after deposition of a specified number of eggs; if unfavourable conditions delay the achievement of this deposit it continues on the resulting sub-optimal level until the fecundity is realized or until the critical age of 50 days is attained. Situations therefore occur in which the rate of reproduction at the older (but < 50 days) ages of the predatory female is larger under sub-optimal conditions than under optimal conditions

Table 24. The influence of the starvation history on subsequent fecundity of four phytoseiid species.

Species	Starvation history			Net fecundity		
	temperature (°C)	food deprivation[a] period (days)	presence of water	$\hat{\mu}$	$\hat{\sigma}$	n
Phytoseiulus persimilis	20	5	no	66.4	11.8	20
		7	no	62.4	14.2	18
		10	yes	69.6	15.4	26
		20	yes	66.4	13.7	16
	30	2	no	60.1	9.4	12
Amblyseius potentillae	20	7	no	28.2	8.1	18
Amblyseius bibens	20	7	no	54.2	10.0	18
Metaseiulus occidentalis	20	7	no	40.8	11.4	18

a. Food deprivation was begun after deposition of 1-3 eggs per female.

at the same age. Examples of this phenomenon are the rate of reproduction of *Amblyseius bibens* at low temperatures (Fig. 15), that of *Metaseiulus occidentalis* at low prey densities (Fig. 14) and that of the same species at unfavourable predator densities (Kuchlein, 1966).

Just before reaching the specified level of egg production a decline in the rate of oviposition takes place. Consequently the rate of reproduction is not related to the female age in a fixed way, but depends on the oviposition history, which becomes relevant after a major part of the eggs has been deposited. For this reason it makes more sense to study the interrelations between the availability of prey, on the one hand, and the searching behaviour and conversion physiology on the other hand (Chapter 3), than to establish age-related reproduction curves under all kinds of conditions. The reproduction curves presented here only serve to validate concepts of the underlying processes (Section 3.1 and Subsection 3.3.5), rather than to be used directly in the population models. However, the data of the potential fecundity are actually used in these models to specify the maximum egg deposit per phytoseiid female.

The data concerning the life span measured at favourable feeding conditions are remodelled before use in simulation. The maximum life span is

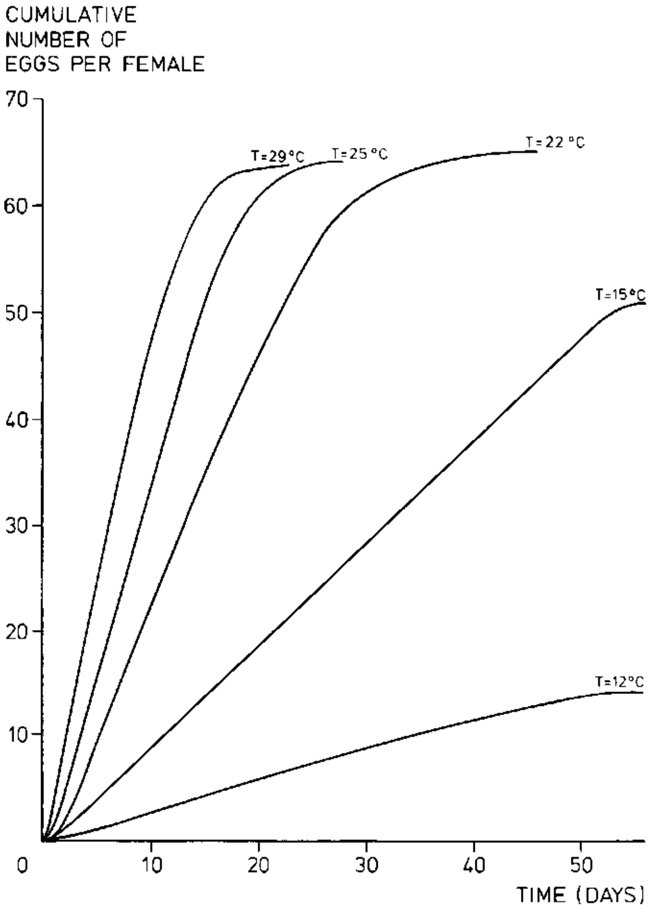


Fig. 15. Cumulative number of eggs produced per living female of *Amblyseius bibens* at different temperature levels and for ample food supply. Data at T = 29, 25 and 22°C are obtained from Blommers (1976).

used instead of the mean life span. This time span is obtained via a least-squares estimate of the 97-99% point of a cumulative frequency distribution of life spans plotted on probability paper of the Gaussian distribution. From this linear equation the relative rate of mortality can be estimated for ten age classes. Similar to mortality of the adult spider mites it appeared from simulations of the population growth (Part 2), that the numerical effects of the temperature dependency could be neglected as well. For this reason the relative rates were smoothed by repeated simulation of the available survival and reproduction experiments until an acceptable overall fit was found. The fitted values are given in Table 25. They show a clear dependency on the relative age (i.e. the age relative to the maximum life span).

Table 25. The smoothed estimates of the relative rate of mortality (day^{-1}) of four phytoseiid species in relation to the age class of the adult female.

Species	Female age class[a]									
	1	2	3	4	5	6	7	8	9	10
Phytoseiulus persimilis	0.004	0.009	0.017	0.042	0.053	0.108	0.170	0.220	0.220	0.320
Amblyseius potentillae	0.006	0.010	0.019	0.038	0.064	0.090	0.150	0.190	0.230	0.320
Amblyseius bibens	0.004	0.008	0.020	0.035	0.071	0.094	0.140	0.220	0.280	0.420
Metaseiulus occidentalis	0.008	0.014	0.014	0.029	0.032	0.042	0.073	0.083	0.112	0.250

a. See Table 27.

Table 26. The effect of prey supply on the relative rate of female mortality (day^{-1}) of *Metaseiulus occidentalis*.T = 27°C; relative humidity = 60-80%. Source: Kuchlein (to be published).

Prey density (number of eggs per 5 cm^2 leaf)	Female age class[a]									
	1	2	3	4	5	6	7	8	9	10
1- 2	0	0	0.010	0.010	0.010	0.010	0.018	0.021	0.026	0.030
4- 10	0	0.004	0.004	0.014	0.014	0.016	0.040	0.050	0.149	0.209
25-150	0.004	0.013	0.017	0.026	0.042	0.043	0.088	0.098	0.101	0.153

a. See Table 27.

Table 27. Smoothed estimates of the duration of an age class in relation to temperature.

Temperature (°C)	Duration of an age class (days)
15	9.0
20	7.0
25	6.0
30	4.5
35	3.3

The effect of the prey supply on survival is incorporated in the population model by appropriate modification of the relative rate of mortality, for which the residence time per age class is held constant. By modelling in this way a low prey supply only causes additional mortality, while the survivors are not affected in any way by their feeding history. The observations on the recovery of starvation (Table 24 and Section 3.1) support this approach. Data on the relative rate of mortality are given in Table 26, but only for the case of *Metaseiulus occidentalis* at 27°C. In the simulations of population growth these data were extrapolated to other temperature levels and used for the four phytoseiid species.

2.2.4 Predation capacity

The reproducing female determines the predation capacity of the four Phytoseiidae in this study: developmental time is short compared to the oviposition period, the sex ratio favours females, and their food intake is considerable because the mean egg biomass produced per day is high compared to the body weight of a mature female. Therefore, the young ovipositing female was chosen for the detailed study of the predatory behaviour of the four Phytoseiidae. To support this choice with quantitative arguments the predation capacity of an individual predator over its whole life span is estimated and the contribution of the reproducing female to this capacity is assessed. Such an estimate can be obtained by taking 'snapshots' of the rate of predation while development and ageing proceeds, and by integrating the rate of predation multiplied by the fraction of surviving predators over the phytoseiid life span.

The measurements of stage-specific predation are presented in Fig. 16. Except for those of *Metaseiulus occidentalis* the larvae were not predacious as confirmed by direct observation of the larval behaviour. The nymphs, males and postoviposition females were much less voracious than the young oviposition females. Simultaneous measurements of the reproduction rate indicated that approximately 70% of the biomass of prey killed is utilized for phytoseiid egg production; for example, a female of *Phytoseiulus persimilis* consumed 6.6 eggs per egg deposited, which corresponds to the results of Ashihara et al. (1978) measured at different temperatures in the range of 10-35°C. Because the food content of a prey egg weighs approximately 1 μg and the egg of *Phytoseiulus* weighs 4.7 μg, the utilization ratio equals to 71%. Thus a rough estimate of the amount of prey eggs killed during the whole oviposition period can be obtained from the net fecundity and the utilization ratio. Furthermore, the amount of prey killed during the other stages can be computed from the product of the stage-specific predation rates and the appropriate mean duration of these stages (Subsection 2.2.1). Taking into account the probability that an individual develops into a female or a male (Subsection 2.2.2) and that it may die from some abiotic

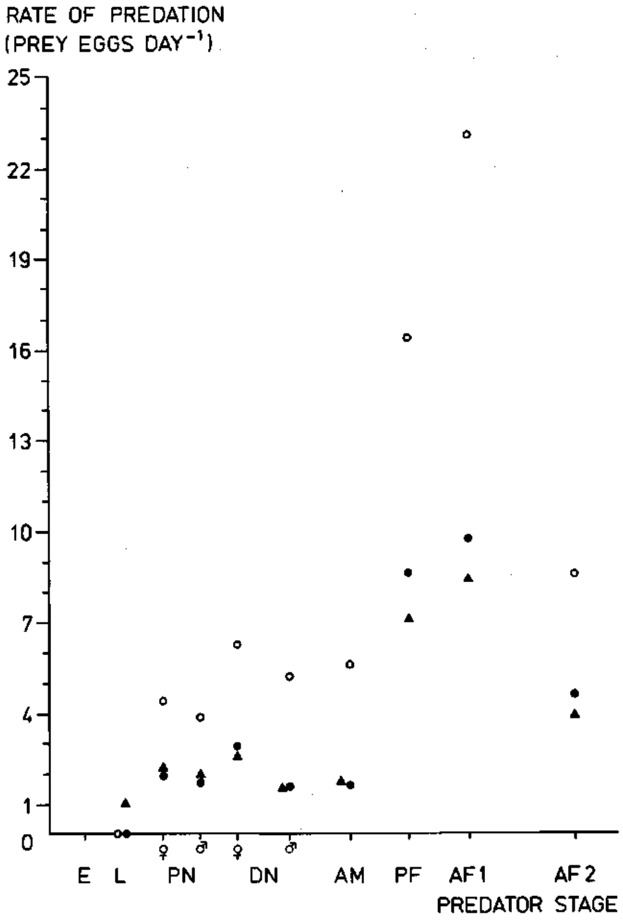


Fig. 16. Stage specific rates of predation of three phytoseiid species for T = 20°C and RH = 75%. o, *Phytoseiulus persimilis*; ●, *Amblyseius bibens*; ▲, *Metaseiulus occidentalis*. Prey egg density = 30-60 eggs/cm²; webbed area = 4-11 cm²; number of replicates = 20-30. E, egg; L, larva; PN, protonymph; DN, deutonymph; AM, adult male; PF, preoviposition female; AF1, oviposition female; AF2, postoviposition female.

cause (Subsections 2.2.1 and 2.2.3), a crude estimate of the predation capacity of an individual predator can be made for each phytoseiid species. The following overall predation capacities (on eggs and larvae) were found:

- *Phytoseiulus persimilis* about 550 prey items each of 1 µg
- *Amblyseius bibens* about 200 prey items each of 1 µg
- *Amblyseius potentillae* about 150 prey items each of 1 µg
- *Metaseiulus occidentalis* about 100 prey items each of 1 µg.

The predation capacity depends on the size of the phytoseiid species: a larger species produces larger eggs and, thus, requires more food for egg growth etc. This is only modified by interspecific differences in fecundity

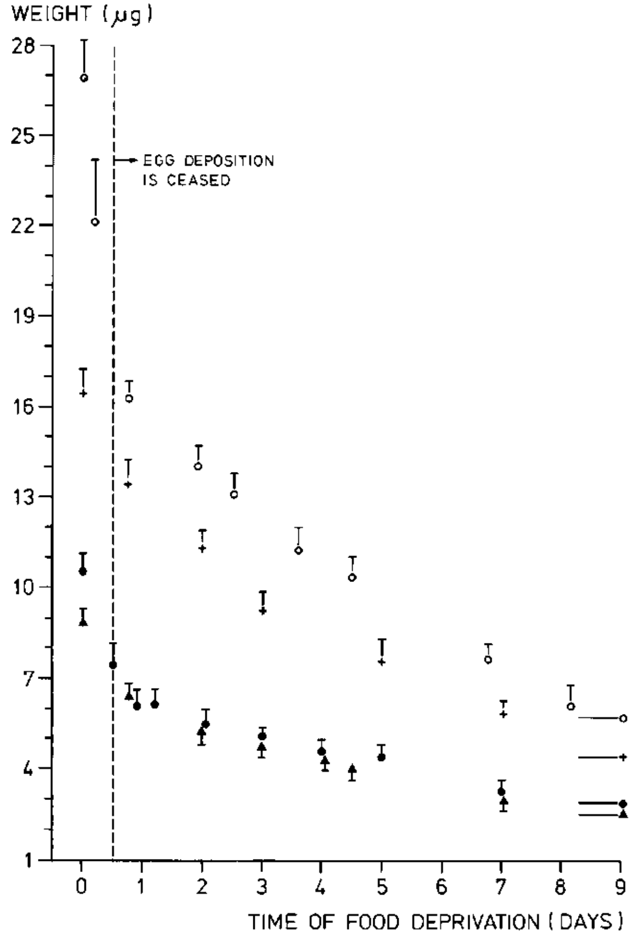


Fig. 17. Weight decrease during the starvation of four phytoseiid species, starting with young well-fed females in the initial phase of their oviposition period. T = 20°C and RH = 60-80%. o, *Phytoseiulus persimilis*; ●, *Amblyseius bibens*; + *Amblyseius potentillae*; ▲, *Metaseiulus occidentalis*; ———, dry-weight levels; ⊥ , standard deviation (n = 20).

and sex ratio, as is demonstrated by the predation capacity of *Amblyseius bibens*, being superior to that of *Amblyseius potentillae*. The contribution of the ovipositing females to these predation capacities amounts to 84, 80, 66 and 60% respectively. Because of this important role of the ovipositing females these were chosen to study interspecific differences in prey searching behaviour (Chapter 3).

2.2.5 Starvation and survival

After depletion of their food source Phytoseiidae are able to survive for some time. When well-fed young females were placed in a Munger cage without any food or water, oviposition initially continued utilizing the food ingested before the start of the experiment, but it ceases within 1 day after one or - less frequently - two eggs had been deposited. Because the weight of an egg corresponds to 20% of the mature female weight, the initial weight decline was very steep, as illustrated by the electrobalance measurements of the female weight during food deprivation (Fig. 17). After egg deposition had ceased, the weight decreased steadily, but much more slowly. Some of the predators were able to withstand severe dehydration. Their body weight approached dry weight, but they did not die. As discussed in Subsection 2.2.3, these starving females are able to recover and subsequently oviposit as well as they did before starvation. The rates of survival during these and other starvation experiments are summarized in Table 28 as the 90, 50 and 5% points of the survival curve. Larvae develop into protonymphs without any food, but after this moult they require food to develop into the next nymphal stage.

Two factors are very important with respect to the rate of survival. First, dehydration is enhanced by an increase of temperature. Second, high humidity and drinking water enables prolonged survival. The role of both factors is demonstrated in Table 28 using additional data from the literature. Because in rose culture the mean temperature is about 20°C and because water spraying takes place frequently, it may be expected that Phytoseiidae are able to survive for 2-3 weeks after the extermination of their prey and in the absence of alternative, non-tetranychid food supply.

Whether non-tetranychid food sources provide a means to survive during a longer period in the greenhouse culture of ornamental roses, will be treated in the remaining subsections of this chapter.

2.2.6 Cannibalism

When other food resources are lacking, the adult female and occasionally the nymphal stages of the Phytoseiidae are reported to feed on their own young, mainly eggs and larvae. The tendency towards cannibalism may differ from species to species and even from population to population. Croft & McMurtry (1972) observed cannibalism among four strains of *Metaseiulus occidentalis* originating from different parts of the U.S.A. They found significant differences in the extent of the cannibalistic behaviour. Laing (1969) reported that when several of each stage of *Metaseiulus* were placed together in a cell, the adults fed on immature stages, but not on each other. He also observed that nymphs of *Metaseiulus* could be reared to maturity on eggs and larvae of the same species. However the resultant adults laid only few eggs

Table 28. The effect of starvation and water supply on the survival of four phytoseiid species.

Predator species	Stage	Temp. (°C)	Approximate time-intervals (days) at x% survival								Reference
			without water				with water				
			90%	50%	5%	n	90%	50%	5%	n	
Phytoseiulus persimilis	AF	10	-	12-25	-	25	-	ca.50	-	25	Hamamura et al., 1978
	AF	20	5-6	6- 7	8- 9	75	9-10	18-19	26-27	75	present report
	AF	22-25	-	8.7	-	33	-	11.8	-	26	Ashihara et al., 1978
	AF	23	-	4(2-5)	-	40	-	15.7 (7-29)	-	40	Mori & Chant, 1966
	AF	26	2.2	3.7	5.6	300	2.2	3.9	5.9	300	Kolodochka et al., 1974
	AF	29	1-2	2	3- 4	45	-	-	-	-	present report
	PN	29	1-2	2	2- 3	40	-	-	-	-	present report
Amblyseius potentillae	AF	20	5-6	7-8	9-10	55	-	-	-	-	present report
Amblyseius bibens	AF	20	5-6	7-8	8- 9	50	-	-	-	-	present report
	AF	22	-	6.8	8.8	19	-	18.8	27.1	26	Blommers, 1976
	AF	28	-	2.1	4.3	67	-	5.1	7.2	66	Blommers, 1976
Metaseiulus occidentalis	AF	20	5-6	7-8	8- 9	41	-	-	-	-	present report
	PN	20	5-6	6-7	7- 8	22	-	-	-	-	present report
	AF	29	1-2	2	3- 4	56	-	-	-	-	present report
	PN	29	1-2	2	2- 3	20	-	-	-	-	present report

AF = adult female predator.

PN = protonymph predator.

and had shorter life spans. In the strain of *Metaseiulus occidentalis* reared by Kuchlein, only very occasionally did hungry females succeed in piercing the egg chorion. This corresponds with observations by Bravenboer (1959). *Amblyseius bibens* may be compared with *Metaseiulus occidentalis* in this respect. According to our own observations *Amblyseius potentillae* becomes cannibalistic to some extent after 1-2 days of food deprivation at T = 20°C. It may then feed primarily on eggs and larvae.

Dosse (1958) was first to report cannibalism in *Phytoseiulus persimilis*. The extent of cannibalism is relatively high in this species: 12 hours of food deprivation at T = 20°C induced cannibalism of eggs; longer periods led to feeding on the larval and nymphal stages. In a starvation experiment with only an initial supply of 30 fresh predator eggs, the longevity of female *Phytoseiulus persimilis* did not exceed the mean value measured in presence of free water in any of the 20 replicates. As expected, the well-fed females deposited one or two eggs during the first day, but only occasionally did egg deposition occur during the next two days. After 3-4 days most of the eggs had hatched. During the subsequent period the water and food content of the larvae and nymphs decreased exponentially with time, until death, as shown for example in Fig. 17. Therefore the food supply decreased drastically during the experiment.

Because the acarine predator-prey interaction frequently leads to rapid local extermination of the prey, the above experiment represents a fairly realistic situation and it may therefore be concluded that in the long run the effect of cannibalism on female longevity does not exceed the effect of water supply. Under the present glasshouse conditions it is reasonable to assume the continuous availability of free water, which thus determines the predator capacity to survive irrespective of cannibalism. However, under dry conditions cannibalism may provide a means for the strongest individuals to survive for some time, when no other food items are available.

Cannibalistic behaviour may be favoured by natural selection, when different generations of the predator are confronted at times with temporary food scarcity. Such a situation can be induced by a high predatory and reproductive capacity of the phytoseiid itself. It will be shown in Part 2 that the capacity of Phytoseiidae indeed leads to local extermination of prey clusters. If neither alternative food nor water sources are available, cannibalism can be expected. It is not surprising, therefore, that especially *Phytoseiulus persimilis* is the most cannibalistic of the species studied here, for the individual weight and the voracity of this species are relatively high and, as will be discussed in Subsection 2.2.7, this predator feeds itself exclusively with Tetranychidae.

2.2.7 Alternative food supply

The Phytoseiidae contain many diverse forms with respect to their feeding habits (McMurtry et al., 1970). Some species seem to be specialized predators of Tetranychidae and show no tendency to reproduce on other types of food. *Phytoseiulus persimilis* is such a species. Although the other species studied could certainly be ranked as specialized predators of Tetranychidae, their dietary range is not restricted to this kind of prey, but includes other plant-inhabiting mites, young stages of various insects and some non-animal foods, like pollens and fungi. A brief review of the literature illustrates the interspecific differences of a number of Phytoseiidae:

- *Phytoseiulus persimilis* is very dependent on the availability of Tetranychidae (Dosse, 1958; Chant, 1961; Ashihara et al., 1978). According to Mori & Chant (1966) the addition of nutritive substances such as sucrose, glucose, pollen, honey and fish meals of various kinds to the drinking water did not significantly increase longevity compared to the effect of water drinking alone. Ashihara et al. (1978) also demonstrated, that *Phytoseiulus persimilis* did not reproduce on honey or pollen (strawberry, castor, red pine), but mean adult longevity was increased to 45 days by nutritional substances such as fresh honey or a 10% sucrose solution, as compared to 12 days with only water available. Laing (1968) reports that strawberry pollen did not promote longevity or development of *Phytoseiulus*, compared to specimens kept without food. Similarly, McMurtry (1977) found that pollen of *Hymenocyclus croceus* was not an acceptable food for this species, in contrast to some other Phytoseiidae.
- *Metaseiulus occidentalis* has been observed to feed, develop and reproduce on tarsonemids (Huffaker & Kennett, 1956; Flaherty, 1967), tydeiids (Flaherty & Hoy, 1971), *Brevipalpus phoenicis*, thrips and some crawler species (Swirski & Dorzia, 1969). According to Flaherty & Hoy (1971), *Metaseiulus occidentalis* could not reach adulthood on Cat tail pollen (*Typha latifolia*), which is an important food for *Amblyseius hibisci* (Kennett et al., 1979). Lee & Davis (1968) reported feeding on this pollen by the adults, but only when Tetranychidae were absent.
- *Amblyseius bibens* is able to rely on certain pollens in absence of Tetranychidae (Blommers, 1976). Among several pollens tested as food for this predator, pollen of some *Papilionaceae* and *Carpobrotus* spp., apple and rose (!) enabled the predator to more or less maintain reproduction. Pollen was the best food substitute. Mass rearing of this predator exclusively on pollen could be continued by Blommers (1976) for more than a year.
- *Amblyseius potentillae* fed and reproduced readily on apple pollen and *Aculus* spp. in the experiments of Kropczynska (1971). Especially interesting are the experiments of McMurtry (1977), which indicated that pollen of *Malephora* was utilized even when an abundance of spider mites was present. For a diet of only pollen, he found a lower rate of reproduction (about

two-thirds the normal rate) and a longer preoviposition period than for only Tetranychidae.

Not all pollens are accepted as food by Phytoseiidae. For example, cotton pollen was rejected as food by *Metaseiulus occidentalis* (Swirski & Dorzia, 1976) and *Amblyseius bibens* (Blommers, 1976), possibly because of its size (75-100 μm) (Kennett et al., 1979). In many other cases it is presumed that the negative responses to certain pollens are related to the chemical or physical nature of their waxy or resinous exine (Kennett et al., 1979).

Several authors state that honeydew can merely serve to promote survival, but allows little reproduction (Huffaker & Kennett, 1956; Chant & Fleschner, 1960; McMurtry & Scriven, 1964, 1965). In an experiment in which a ^{32}P solution was mixed with bee honey and offered as droplets to hungry young females of the phytoseiid species in hunger cages, the degree of ^{32}P ingestion was measured with the aid of the Cherenkov-method. The results indicated that *Amblyseius potentillae* was far more able to ingest the honey (500-2000 counts per minute) than the other species, even when these were starved for long periods (*Amblyseius bibens* 100-200 counts per minute; *Metaseiulus occidentalis* 50-100 counts per minute; *Phytoseiulus persimilis* 0-50 counts per minute).

From the review of the literature the degree of specialism on tetranychid prey can be derived using the preference for the different pollens relative to tetranychid prey as a criterion. As stated before, *Phytoseiulus persimilis* is highly specialized on tetranychid prey, which is also true for *Metaseiulus occidentalis* and *Amblyseius bibens* but especially the latter species is able to rely on non-animal food when tetranychids are absent. *Amblyseius potentillae*, however, seems to accept both pollen and tetranychids when offered simultaneously. The original criterion thus leads to a sequence that corresponds with that obtained from the ^{32}P ingestion experiments.

The short survey above indicates differences in the dietary range that may be important for their survival and reproduction in a natural habitat. It may be important too in the greenhouse culture of ornamental roses, but the hairless rose-leaves are less suitable as pollen gathering centres and, besides, other plant feeding arthropod or honeydew are absent and/or undesirable. It was therefore presumed, that under the greenhouse conditions to be investigated, the effects of an alternative food supply will not exceed that of simple water supply to an important extent. This presumption was confirmed by release experiments with the four phytoseiid species. Fifty young ovipositing females were released on a group of five potted rose bushes upon which 1-2 gram of fresh *Vicia* pollens had been scattered. The roses were sprayed daily with water. The rate of survival was measured in two ways: by direct inspection of the leaves; and, if this method indicated low numbers of predators, by inspecting mite infested bean leaflets 10 hours after being pinned on to the rose leaves (10 leaflets per bush). If both checks rendered negative results, the predators were assumed to be absent.

Table 29. Survival of young phytoseiid females of four species on rose bushes scattered with pollen. T = 17-22°C; relative humidity = 60-80%.

Species	Number of predators found by direct inspection of leaves				Number of predators found by trapping in mite colonies on bean leaves pinned onto the rose leaves
	Number of days after release				Number of days after release
	10	15	21	29	29
Phytoseiulus persimilis	21	13	2	0	0
Amblyseius potentillae	33	27	6	0	0
Amblyseius bibens	43	36	8	0	1
Metaseiulus occidentalis	45	29	3	0	0

Survival appeared to be not significantly promoted by the pollen treatment (Table 29); it did not exceed the survival expected under conditions of water supply and the actual climate (T = 17-22°C; relative humidity = 60-80%). However, Blommers (1977) found positive effects of the pollen treatment on the survival of *Amblyseius bibens*, even at a high temperature (T = 28°C). He used peanut plants amply populated with predators shortly after they exterminated the spider mite population on these plants. Consequently these plants were covered by some (sticky) webbing, which may serve as a better pollen gathering centre than the bare rose leaves. This report does not, however, treat this aspect.

Although it seems difficult to maintain the predator population permanently by the addition of nutritional substances, the survival of even the most specialized phytoseiid, *Phytoseiulus persimilis*, may be promoted by spraying 10% sucrose solutions (Ashihara et al., 1978). This possibility should be evaluated under greenhouse conditions.

3 Predation, reproduction and residence time in a prey colony

As argued in Chapter 2 the predation capacity of phytoseiid predators is largely determined by the high rate of food conversion during the oviposition period; under favourable conditions phytoseiid females are able to produce an egg biomass per day equal to their own weight. The rate of reproduction will therefore depend on the searching efficiency of the predator and the availability of the prey. It was outlined, moreover, that previous reproductive success (i.e. the number of eggs already deposited) is more important in determining future reproductive food demands than ageing. Apparently, among Phytoseiidae there is a tendency to deposit a specified number of eggs. Because the availability of prey is not uniformly distributed in space, the food demands of the ovipositing female may lead to moving from colony to colony in search of a satisfactory supply of prey and a minimized level of interference with other conspecific females.

The availability of the two-spotted spider mite is restricted to the plant area covered by webbing. The webbed area is generally situated at the lower side of the leaves and is arbitrarily subdivided in units surrounded by uncolonized parts of the leaf. These so called colonies attain their maximal size when the underside of the leaf is completely webbed.

During the residence of the predator in a certain colony, prey consumption will lessen the local supply of prey until the predator leaves the colony, because of the lower level of prey availability. In search of new prey colonies, the predators tend to aggregate at colonies with high prey supply, but this aggregative response may be counteracted by mutual interference among the predators, which enhances the tendency to disperse from the colony, independent of the local prey supply. Moreover, mutual interference can lead to a decreased rate of reproduction, as shown by Kuchlein (1966).

In this chapter the relation between on the one hand prey and predator density in the colony and, on the other, the rate of predation, reproduction and departure is analysed. This analysis is confined to the level of a female predator foraging in a colony of spider mites. Those aspects of foraging behaviour that take place after departure from a colony are treated in Part 2 of this Agricultural Research Report, as well as the aspects concerning population growth.

The analysis is carried out by validation of conceptual models of predatory behaviour. A predation model is constructed that is based on random searching periods between successive encounters with prey items and on a relation between the motivational state of the predators (Section 3.1) and the prey density related rate of successful capture (Section 3.2). The indicator of the motivational state of the predator is chosen to be the food content of its gut. According to Akimov & Starovir (1978) the gut walls of phytoseiids are markedly extensible, compared to other gamasids. Nevertheless there has to be a maximum load, whether this is caused by a limited extensibility of the body or gut walls, or by a negative feedback to feeding via gut or body wall stretch receptors, as found in *Phormia regina* by Gelperin (1971) and Belzer (1979). Because ingestion, maximal gut content and gut emptying may be quantified by use of the electrobalance, the food content of the gut can be related to behavioural components by observation of the predatory behaviour and simultaneous calculation of the amount of food present in the gut.

The behavioural components needed to calculate the rate of encounter at any level of the motivational state and prey density are as follows:

- width of the searching path (cm)
- distance of prey detection (cm)
- walking speed (cm/s)
- walking pattern
- walking activity (%)
- coincidence between prey and predator in the webbed space
- success ratio (%)
- handling and feeding time (s).

The relations between the motivational state of the predator and these behavioural components are used in a simulation model of the queueing type (Taylor, 1976; Curry & DeMichele, 1977), where the predator is considered to be the service facility, i.e. 'the dentist', and the prey 'the client', who may enter (at a certain rate) the 'waiting room' (i.e. gut) in expectance of the service (i.e. 'digestion, absorption and egestion').

In another model the walking behaviour is simulated to calculate the rate of encounter between predator and prey or the rate of departure from the prey colony (Sections 3.2 and 3.4) on the basis of measurements of the above components of walking behaviour. Video equipment enabled the registration of the walking pattern, which was used to measure the walking velocity and the frequency distribution of changes in walking direction after a fixed step size. The model simulates the walking behaviour on basis of the assumption that the direction of each step deviates from the direction of the previous step with an angle chosen at random from the experimentally defined frequency distribution, autocorrelations being accounted for. The calculation of the rate of predator-prey encounter serves to estimate the effect of recrossing the areas already searched by the predator. The calculation of the rate of departure from the colony serves to elucidate the role of patch specific cues in the intracolony residence time of the predator.

Apart from fundamental ecological interest in analyzing the foraging behaviour, there are more reasons to undertake a detailed component analysis instead of direct measurement of the resulting rate of predation. Extrapolation of the measured prey consumption to the population level is only allowed if the motivation of the predator is in a steady state during these measurements of the rate of predation, as well as during population growth of predator and prey. Rabbinge (1976) solved the first problem by allowing the predator to adapt its motivational state to a constant prey density before measurement of the rate of predation. Prey density was kept constant by replacement of the prey captured (or died from other causes) at 15 min intervals. However prey replacement is essentially impossible in the webbed colony, because mite transfer with the aid of a brush can damage the web structure and can disturb the predator being sensitive to movements of the web. Numerical simulation of the predation on the basis of a component analysis may provide a means to keep track of a changing prey density and to estimate predation at constant prey density. With respect to the extrapolation of predation measurements to the level of population growth - the second problem - Rabbinge (1976) assumed instantaneous equilibration of the phytoseiid motivation to any change in prey density. This assumption is tested in Part 2 of this Agricultural Research Report by using a simulation model of population growth and dispersal of prey and predator that can account for non-steady states of the motivation.

Finally, the component analysis was undertaken to study the role of webbing in the acarine predator-prey interaction. In most of the reported experiments webbing was either not included or it was distributed in an unrealistic way due to the flat and artificial substrates (paper, plastic) or due to the stage of the prey, which produced a web different from that of the adult female. Although female-produced webbing has a very chaotic structure, it can be considered as a coherent unit (Figure 8), which should be distinguished from the uncolonized parts of the leaf in acarine predator-prey studies.

Actually some unexpected types of functional response of phytoseiid predators to the density of their prey were attributed to clumped distributions of webbing in space (Mori, 1969; Fransz, 1974). Other deviating forms of the functional response were attributed to disturbance of feeding predators by active prey, resulting in an attack on the interfering prey, that bumped into it (Sandness & McMurtry, 1972), or attributed to contact disturbance, decreasing the number of successful captures (Mori & Chant, 1966). Kuchlein (to be published) found a second rise of the functional response of *Metaseiulus occidentalis* at high prey egg densities. Probably this phenomenon was not related to the food satiation level of the predator, but rather to a contact stimulus. However it may be questioned whether the above behavioural factors operate in the webbed area. Preliminary observations indicated that both predator and prey were less active in the prey colonies and disturbance of the predator was rarely observed. Furthermore, webbing may change predation simply by surface enlargement or by inducing specific changes in the predatory behaviour, as discussed in Subsection 2.1.6. Therefore detailed observation of predation was preferred.

3.1 DYNAMICS OF THE MOTIVATIONAL STATE

By assuming the food content of the gut to be the main indicator of the motivational state of the predator, the dynamics of the predatory motivation can be simulated by integration of the rate of ingestion (Subsection 3.3.1) and the rate of gut emptying (Subsection 3.1.2). This simple concept allows the calculation of the motivational state during observation of the predatory behaviour, so that predatory motivation and behavioural components can be related to each other (Section 3.2). These relations are used in turn in the predation models to calculate the rate of predation (Section 3.3). Validation of this type of predation models did not result in a rejection of the concept (Holling, 1966; Nakamura, 1974; Fransz, 1974). However the postulation of one intervening variable, indicating the hunger drive, may be too simple a hypothesis to account for all hunger related behaviour. For example it may be questioned, whether the motivational state adapts itself instantaneously to a change in the food content of the gut. In other words does a certain level of gut filling induce the same searching behaviour, whether it is achieved via ingestion or gut emptying starting from low or large amounts of food in the gut respectively? This problem is considered at some occasions in this chapter (for example Subsection 3.2.7). Another problem concerns the quality of the food. The existence of specific hungers for proteins, sugars or water has been shown in the blow fly (Dethier, 1976). Because phytoseiids are known to rely on pollens, honeydew and water apart from tetranychids and because the developmental stages of the spider mite may not have the same food quality to the predator, diet composition may be relevant in defining the motivational state of the predator. However a detailed quantitative understanding of the metabolic consequences of diet composition for absorption, synthesis and allocation of food elements does not yet exist, even for insect physiologists pets. For the time being the food content of the gut will be expressed in terms of weight (μg), assuming the quality of the ingested food to be constant. In Subsection 3.1.3 this assumption is criticized on the basis of available references pertaining to diet composition and phytoseiid reproduction.

The phytoseiid females used for the experiments were all treated in the same way. They developed on bean leaves with an abundance of *Tetranychus urticae* at all developmental stages (T = 25°C, relative humidity = about 75%). Female deutonymphs were collected from this stock and transferred to other leaves with abundant food (T = 20°C), where they moulted and copulated after supply of males. When the female predators had deposited their first eggs, they were ready for experimentation. Subsequently, whenever these predators were deprived of food, care was taken to use only satiated predators by sampling them immediately after an actual feeding period. Next they were put individually in Munger cages (Figure 10) for different time intervals and at different temperatures, depending on the particular purpose of the experiment. Unless stated otherwise, the female predators never exceeded the age of 10 days as an adult.

3.1.1 Ingestion

After a successful capture the predator starts ingesting the prey content, the movements of the ingested fluid being visible through its transparant body wall. Presumably praedigestive fluids are injected for extra-intestinal digestion (Akimov & Starovir, 1975). The amount of food ingested depends on the following factors:

a - the amount of food that can be ingested by one or more predators from a single prey stage (the ingestable food content of the prey)

b - the suction force in relation to the phytoseiid species involved and the fluidity of the food (the ingestion constant)

c - the difference between the maximum food content and the actual food content of the gut of the predator (the satiation deficit of the gut)

d - the sum of the periods in which the mouth parts of the predator are intruding the body of the prey (the feeding time, Subsection 3.2.8).

a As a first approximation of the ingestable food content of the prey one

Table 30. The ingestable food content of the developmental stages of *Tetranychus urticae*.

Prey stage	Weight increase (μg) after feeding									Fresh weight minus dry weight[a]
	Metaseiulus occidentalis			*Amblyseius potentillae*			*Phytoseiulus persimilis*			
	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n	$\hat{\mu}$	$\hat{\sigma}$	n	
egg	1.0	0.2	30	-	-	-	-	-	-	0.8
larva	1.1	0.2	24	1.1	0.2	12	-	-	-	1.3
protonymph	-	-	-	2.3	0.3	14	-	-	-	2.7
deutonymph♀	2.9	0.2	16	5.1	0.3	30	7.3	0.5	21	8.6
male	-	-	-	2.5	0.2	27	2.4	0.3	17	2.7
female	2.8	0.4	18	4.9	0.4	16	7.8	0.5	29	17.9

+tab 12
bh 29

a. According to the data of Mitchell (1973).

could measure the difference between the fresh and the dry weights of the different prey stages. These estimations can be obtained from the work of Mitchell (1973). A more precise method is to compare the weights of an initially hungry predator (2 days starvation at T = 20°C) before and after feeding on a certain prey stage. The results of both types of measurements are given in Table 30, which shows correspondence only with respect to the small prey stages. Because the amount of food ingested from the adult female prey increased with the body size of the phytoseiid species, one may suppose the ingestable food content of this stage to be much higher. In an experiment with females of *Phytoseiulus persimilis* and *Tetranychus urticae* the total weight of food consumed by three hungry predators from one single prey amounted to 16.6 μg, which result closely approximates the estimate based on the difference between the fresh and dry weight of the prey. Apparently the amount of food in the female prey exceeds the maximal food content of the phytoseiid gut. It can therefore be concluded, that the ingestable prey content per single predator is limited by both prey size and gut size.

In another series of experiments ingestion was measured in relation to feeding time. By interruption of feeding after fixed time intervals the amount of food ingested by a hungry predator can be monitored with the aid of the following methods. The first method is to measure the weight of the predator before and after a predetermined feeding period. However this method is not reliable, when the weight differences are below 0.5 μg, as e.g. in the egg stage. In that case another method was applied using ^{32}P-labelled prey. The spider mites were labelled by feeding during 12 hours on a bean leaf, previously put with its stem in a ^{32}P solution (1 mCi) for 1 day. Radioactive eggs were obtained from radioactive females. The labelled prey was offered to an unlabelled female predator, being deprived of food for 2 days at T = 20°C since satiation. Fransz (1974) assumed, that the amount of radioactivity in the prey was proportional to its food content. However the author's experiments indicated such a high variability among prey individuals of exactly the same age and labelled on the same bean leaf that this assumption is invalid. This variability may be due to the unhomogeneous distribution of ^{32}P in the leaf or to individual differences in sucking activity of the mites. Therefore the ingestion experiments with ^{32}P labelled prey can only be interpreted, when the radioactivity ingested by the predator is expressed as a fraction of the total radioactivity initially present in the individual prey. For this reason the exploiter and its victim were brought into separate glass vials after a predetermined feeding period. Subsequently they were crashed by means of a glass stick and their contents were dissolved in 10 ml water. These vials were brought into a radioactivity counter, which directly registers the β-radiation emittance of ^{32}P by means of the Cherenkov method. The neutrons emanated by the ^{32}P molecules were counted during 10 minutes and next corrected for the mean number of counts registrated in vials containing only water. The proportion of the total radioactivity ingested by the predator can be computed from these counts and this indicates the level of ingestion. The shapes of the ingestion curves obtained by the above methods were invariably of the saturation type. Therefore the following formula was adequate for description of the fraction ingested relative to maximal (i.e. uninterrupted) ingestion:

$$\text{Fraction ingested} = 1 - e^{-\mathrm{RRFI} \cdot \text{time}}$$

RRFI = relative rate of food intake (time^{-1})

In this formula RRFI represents the resultant of the suction force (or ingestion constant) of the predator and the viscosity of the prey content. The value of this ingestion constant can be estimated from the slope of the linear regression of $\ln(1-FI)$ on time. These estimates are given in Table 31. Apparently the ingestion constants do not differ very much between the species studied. However, one exception must be noted in case of *Amblyseius potentillae* attempting to ingest the content of the tetranychid egg. For some reason this predator has difficulties in puncturing the egg chorion, as suggested by direct observation of the predatory behaviour. Kuchlein (personal communication) measured a much lower rate of reproduction of this predator: if eggs of *Tetranychus urticae* in stead of larvae were offered as prey. This result corresponds with the measurements of ingestion that indicated no absolute barrier to ingestion, but some hindrance when compar-

Table 31. The ingestion constants RRFI (min^{-1}) of four phytoseiid species in relation to the stage of the prey.

Predator species	Egg		Larva		Proto-nymph		Deuto-nymph ♀		Male		Female	
	$\hat{\mu}$	n	$\hat{\mu}$	n	$\hat{\mu}$	n	$\hat{\mu}$	n	$\hat{\mu}$	n	$\hat{\mu}$	n
Metaseiulus occidentalis	1.9	27	1.1	10	-	-	0.11	10	0.7	12	0.07	18
Amblyseius bibens	1.8	12	-	-	-	-	-	-	-	-	-	-
Amblyseius potentillae	0.2	52	0.8	9	0.6	26	0.3	14	0.4	21	0.15	24
Phytoseiulus persimilis	1.8	38	-	-	0.9	37	0.4	30	-	-	0.05	11

NB. The correlation coefficients vary between 0.84 and 0.91; the intercepts are not tabulated as they are close to zero.

ed with the other phytoseiid species. Another conclusion can be drawn from the measurements in Table 31 with respect to the effect of the prey stage on the ability to ingest its content; the more development proceeds, the more difficult it is for the predator to suck the prey content. This may be caused by the internal structure of the body being very compartimentalized in the adult female phase. Another explanation may be found in relation to the time required for extra-intestinal digestion of solid structures. Despite these differences in the measured ingestion constants it can be stated, that 90% of the overall ingestion per prey takes place during the initial 20% of the prey stage specific feeding times of the different predator species (Subsection 3.2.8). Because the feeding times are rather short and, therefore, also the period needed for 90% food intake, it is not far from reality to consider the ingestion process as an immediate swallowing of the food content of the prey. This concept is a prerequisite for the queueing approach of the predation process, to be discussed in Subsection 3.3.1.

Several times observations indicated, that even small prey were not consumed completely, as also reported by Lee & Davis (1968), Fransz (1974) and Rabbinge (1976). Rabbinge presented indirect evidence for this phenomenon. By assuming that ingestion by the predator equals its gut emptying on the average at a constant prey density, he estimated the prey-utilization from this equation after measurement of the rate of predation and gut emptying. These indirect estimations pointed to the importance of partial ingestion of the prey content. Direct proof was given by the following experiments, using the electrobalance. Females of *Phytoseiulus persimilis* were deprived of food for different periods starting from full satiation and subsequently a female of *Tetranychus urticae* was offered as prey. The difference in the weight of the predator before and after feeding were measured with the electrobalance and the results are plotted in Fig. 18. A similar

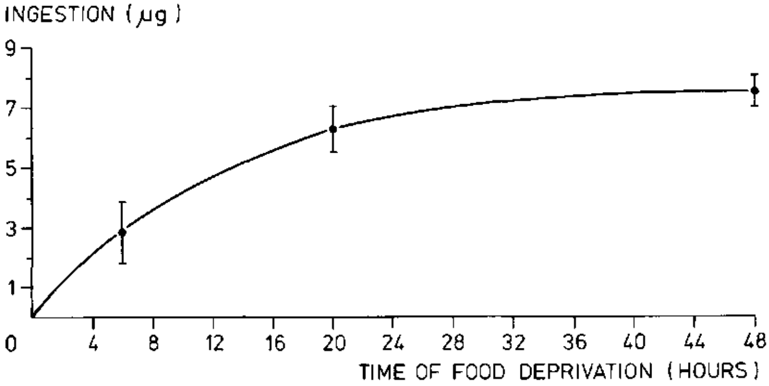


Fig. 18. Weight of the food ingested by young females of *Phytoseiulus persimilis* from females of *Tetranychus urticae* after different periods of food deprivation (T = 20°C). ⊥ = standard deviation.

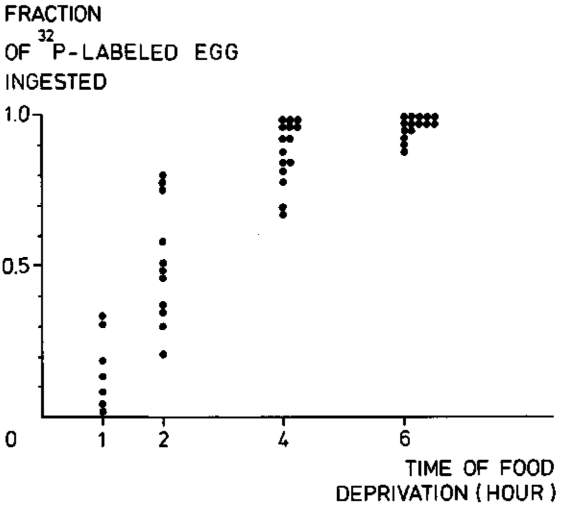


Fig. 19. Proportion of radioactivity ingested from a ^{32}P-labelled egg of *Tetranychus urticae* by individual young females of *Metaseiulus occidentalis* after different periods of food deprivation (T = 20°C).

experiment was done with females of *Metaseiulus occidentalis* and ^{32}P-labelled eggs of *Tetranychus urticae* (Fig. 19). Both experiments demonstrate the occurrence of partial ingestion. Moreover the shape of the ingestion curve is of the saturation type instead of sigmoid, which suggests that the predator tends to empty its prey as far as allowed by the satiation deficit of its gut or the food content of its prey.

As discussed before, the amount of food in the adult female spider mite largely exceeds the phytoseiid gut volume. In this way an estimate of the gut volume was already available. However a second estimate was needed, because the apparent gut volume may depend on the prey stage involved. This was accomplished by allowing hungry phytoseiid females (2 days food deprivation at T = 20°C) to feed on eggs and larvae instead of feeding on adult female prey until they were satiated. Satiation was defined by the occurrence of at least 10 successive contacts of the predator with its prey without subsequent attack. The weight difference between the predator before and after feeding until satiation was measured using the electrobalance to estimate the apparent gut volume in case of small prey stages. Predators unable to achieve satiation within two hours were discarded to prevent overestimation of the volume due to gut emptying by absorption or egestion. The results indicated only a slight influence of the prey stage on the estimated gut volume, as shown in Table 32. Therefore this aspect was neglected in further analyses for the sake of simplicity. Moreover the results indicate that the interspecific differences in gut volume are proportional to their size, as expected.

In summary, the ingestion process can be considered as an immediate swal-

Table 32. The apparent gut volume of four phytoseiid species, estimated from the weight increase of hungry female predators after feeding on eggs and larvae of *Tetranychus urticae* until satiation.

Phytoseiid species	Weight increase (µg)		n
	$\hat{\mu}$	$\hat{\sigma}$	
Metaseiulus occidentalis	3.2	0.2	25
Amblyseius bibens	3.3	0.2	15
Amblyseius potentillae	5.2	0.4	32
Phytoseiulus persimilis	8.1	0.4	38

lowing of the prey. The amount of food consumed is determined by the available space in the gut or the food content of the prey, depending on which of both factors is the smaller one. To inlcude this aspect the previous ingestion formula can be extended as follows:

$$\frac{I_{FT}}{IF} = 1 - e^{-RRFT \cdot FT} \quad \text{and} \quad IF = \min(SDG, FCP)$$

FT = feeding time
I = ingested food
IF = ingestable food content of the prey per predator
SDG = satiation deficit of the gut
FCP = ingestable food content of the prey

3.1.2 Gut emptying

The rate of gut emptying can be measured by weighing the amount of food required to satiate the predator after different periods of food deprivation. After a certain hunger period the predators were 'drugged' by a slight amount of CO_2 to reduce their mobility and weighed using an electrobalance. Next they were brought to a feeding area, consisting of a prey colony with abundant numbers of eggs and some females, where they were allowed to feed until satiation. After a certain number of successful attacks predators tend to leave prey unharmed, despite contact with the predators' front legs. When 10 successive failures of this kind were recorded, the predator was considered to be satiated. To prevent overestimation of the food consumed, due to gut emptying, this series of events had to take place within a short time interval. Predators requiring more than two hours (T = 20°C) to achieve satiation were therefore not considered. After an anaesthetic, the final weight of the predator was measured and the weight increase after the hunger period in question could be calculated.

The results of these experiments are shown in Figure 20 for young females of *Phytoseiulus persimilis*, at three different temperatures. In agreement with Holling (1966) and Green (1965), the results show that the gut is emptied in an exponential fashion:

$$FE = 1 - e^{-RRGE \cdot time}$$

FE = fraction emptied
$RRGE$ = relative rate of gut emptying ($time^{-1}$)

Moreover, temperature is an important factor influencing the rate of gut emptying. The RRGE values estimated from the measurements were almost in a straight line when plotted against temperature (RRGE in day^{-1} = 0.21 × (temperature - 11°C). Moreover these estimates show that the ingestion constant is much larger than the relative rate of gut emptying viz. 70-2700 per day compared to 1-4 per day.

Although this experimental procedure did produce some useful results, there were some problems in applying it for all the species in question. Weighing of the individuals before and after feeding was rather difficult, because they were easily disturbed by the manipulations during transport causing a delay in the achievement of full satiation. Besides, the time period allowed for the achievement of satiation made it necessary to discard almost 60% of the replicates from the final results. Therefore some alternatives were applied. The first method was to omit the weighing proce-

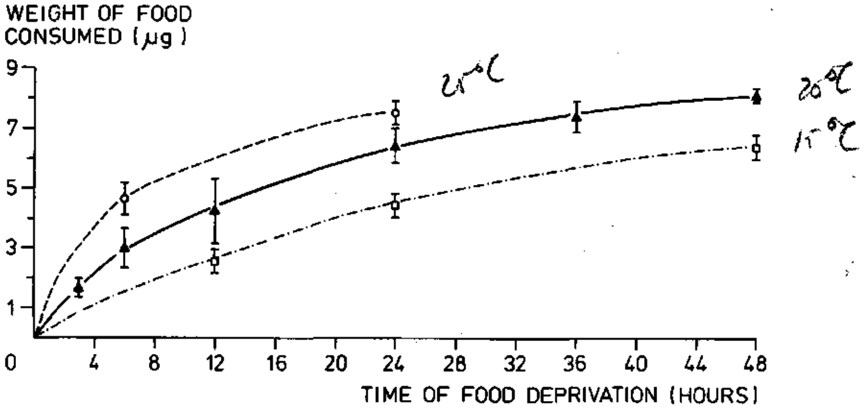


Fig. 20. Weight of the food consumed until satiation by young females of *Phytoseiulus persimilis* after different periods of food deprivation and at three temperature levels. o, T = 25°C; ▲, T = 20°C; □, T = 15°C; ⊥ = standard deviation.

dure and to feed the predator merely with eggs. A simple enumeration of the number of eggs consumed and the data on the ingestable food content provided a way to estimate the ingestion until satiation, thereby neglecting partial ingestion. Although the procedure was much more simple, the criterion for full satiation remained a central problem to obtaining replicates easily. Therefore another method was developed, based on the energy expenditure in the phytoseiid physiology.

As discussed in Subsection 2.2.3, the phytoseiid female is capable of producing a daily egg mass equal to her own weight. Obviously the level of energy conversion is quite high in the oviposition phase. Therefore it may be expected that the rate of absorption of digested food into the haemolymph is closely linked to the rate of reproduction. According to Treherne (1967) and House (1974) the absorption of amino acids and sugars from the gut differs from that of the vertebrate intestine in that these substances do not appear to be absorbed by specific active transport mechanisms against concentration gradients. With respect to lipids, there are also no valid *a priori* reasons for active transport across the gut wall, as argued by Treherne (1967). The net absorption appears to be linked to water movements and to result from the concentration gradients developed across the gut wall due to the uptake of water into the haemolymph. These water movements can be the result of osmosis and arthropods are capable of performing osmotic work (Berridge, 1970), so that absorption of gut stores may even occur against concentration gradients between the gut fluid and the haemolymph. However these mechanisms could be overruled by diffusive absorption induced by the withdrawal of blood stores. A rapid conversion of amino acids to proteins and monosaccharides to disaccharides will tend to maintain a steep concentration gradient across the gut wall. Thus, because the absorbed food elements are utilized in egg formation and fuel supply the rate of absorption will be related to these processes too in case of a high turnover of energy. Hudson (1958), for example, has shown that the delivery of gut stores is greatly speeded by increased energy expenditure, as for example flight. Similarly, the withdrawal of water molecules from the (hind)gut into the blood will influence the concentration gradient and will be related to water loss from the body due to transpiration and oviposition. Therefore it is very probable that the absorption rate in phytoseiid females, which have a high rate of reproduction, will be closely related to egg formation and transpiration, and, of course, *vice versa*.

The rate of absorption will probably dominate the rate of gut emptying, for the presence of a colon and Malphigian tubules (Akimov & Starovir, 1975) indicate some degree of recycling of the water, as opposed to the gut structure of the two-spotted spider mite (Subsection 2.1.4). A rough estimate of the egestion rate on basis of the size of fresh faeces droplets and the frequency of defaecations of a satiated female *Phytoseiulus* resulted in a value of the egestion constant that is 5% of the relative rate of gut emptying.

Based on the above, tentative reasoning, the relative rate of absorption (RRA) can be estimated from the balance between ingestion and weight loss. Under conditions of abundant food the gut will approach satiation, and because the gut volume is measured (Subsection 3.1.1), RRA can be fitted such that the rate of absorption compensates the weight loss occurring under these circumstances. The weight loss due to egg production can be estimated from the specific weight of the phytoseiid egg and the measured rate of oviposition. As well, an approximation of the weight loss due to respiration and transpiration can be obtained from the weight decreases measured in the starvation experiments presented in Subsection 2.2.6. The estimation of the relative rate of absorption is carried out with a simulation model in which RRA is the only unknown parameter, while the output consists of the rate of oviposition. The structure of the model is based on the principle that arthropods avoid gluttony, so that there may be an optimal body weight above

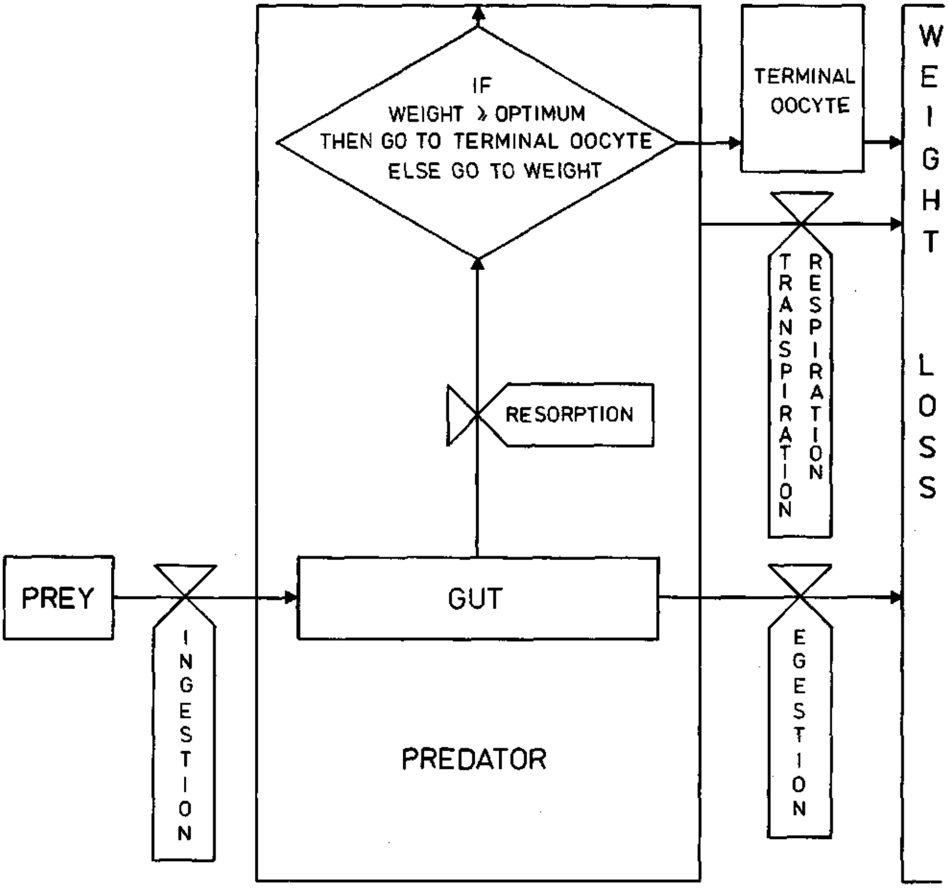


Fig. 21. Flow diagram of phytoseiid energy expenditure, relating ingestion to oviposition.

which the absorbed food is spent on egg formation and below which it is spent on compensation of weight loss due to respiration and transpiration. Because the terminal oocyte absorbs the major part of the lipoproteins and water, egg production can be simulated by extrusion of the egg, if the specific weight of the phytoseiid egg is achieved. A flow diagram of this simple concept of the relation between ingestion and reproduction is presented in Fig. 21; the program is listed in Appendix A. With this model, the relative rate of absorption can be fitted such that the rate of oviposition calculated by the model corresponds with that measured experimentally. The experimental values of the oviposition (Fig. 22) were measured at several temperatures in a colony with abundant numbers of prey eggs for young female predators of *Phytoseiulus persimilis* and *Metaseiulus occidentalis*. The oviposition data concerning *Amblyseius bibens* and *Amblyseius potentillae* were obtained from Blommers (1976) and Rabbinge (1976). The results are presented in Table 33. These show that *Metaseiulus occidentalis* and *Amblyseius bibens* resemble *Phytoseiulus persimilis* greatly with respect to the estimated values of RRA, but that *Amblyseius potentillae* has a much lower level of energy conversion, because of its lower rate of egg production. Moreover, for *Phytoseiulus persimilis* it can be concluded that the RRA estimates obtained by the present curve fitting procedure correspond very closely with the estimates of RRGE (= RRA) obtained by adequate use of the electrobalance. This correspondence may justify further use of the RRA values obtained for the other phytoseiid species by the curve fitting procedure.

Because these model estimations of RRA were obtained from reproduction

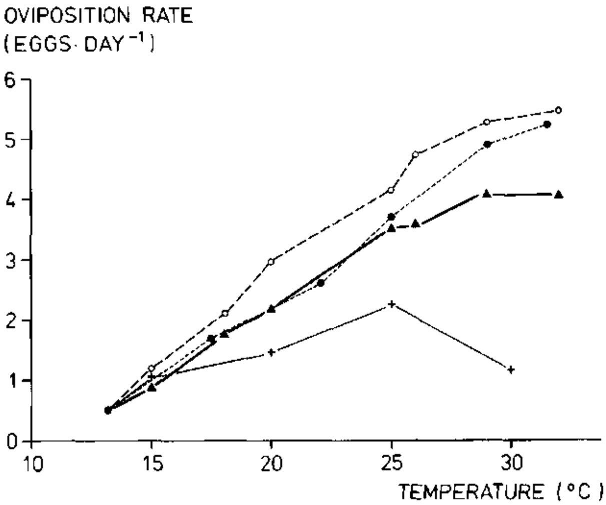


Fig. 22. Rate of oviposition of young females of four phytoseiid species in relation to temperature (abundant food). o, *Phytoseiulus persimilis* (n = 32); ●, *Amblyseius bibens* (Blommers, 1976); ▲, *Metaseiulus occidentalis* (n = 25); +, *Amblyseius potentillae* (Rabbinge, 1976).

Table 33. Indirect estimations at different temperatures of the relative rate of absorption (day^{-1}), based on the weight balance of a phytoseiid female (see Figure 22).

Predator species	Temperature (°C)									
	13	15	18	20	22	25	26	29	30	32
Phytoseiulus persimilis	-	0.86	1.50	1.98	-	3.08	3.33	3.87	-	3.99
Amblyseius bibens	0.31	-	1.32	-	1.86	2.55	-	3.33	-	3.88
Metaseiulus occidentalis	-	0.72	1.33	1.62	-	2.54	2.55	3.15	-	3.21
Amblyseius potentillae	-	0.76	-	1.26	-	2.10	-	-	1.52	-
Relative rate of colour decrease *A. potentillae* (Rabbinge, 1976)	-	0.45	0.68	0.78	-	1.01	-	-	1.46	-
Relative rate of gut emptying of *M. occidentalis* (Fransz, 1974)	-	-	-	-	-	-	10.44	-	-	-

experiments for abundant food supply, it is worthwhile to compare the rate of oviposition calculated by the model for lower levels of food supply with those measured in matching experiments. The model uses the RRA value estimated at abundant food supply and the rate of predation measured at suboptimal levels of food supply, but the rate of oviposition is calculated for lower food supply levels for comparison with the measured reproduction. Two comparisons concerning *Metaseiulus occidentalis* and *Amblyseius potentillae* are presented in Tables 34 and 35. The results show a close correspondence between the calculated and measured oviposition, which demonstrates the usefulness of the estimated RRA values. Apparently the gut is emptied in an exponential fashion, as was also found by direct measurement for *Phytoseiulus persimilis*. In the simulation model, the time required for transport, synthesis, utilization and allocation of the absorbed gut-stores in the acarine body is not considered, because it was assumed that each molecule absorbed was matched by simultaneous utilization of another molecule. This assumption was tested in two experiments concerning the reaction of the reproduction on sudden changes in food supply. The first experiment consisted of the measurement of the numerical response of *Metaseiulus occidentalis* to sudden changes in prey egg density, using two levels of food supply, both giving rise to some level of reproduction. The measurements carried out by Kuchlein were compared with matching simulations based on

Table 34. Simulated and measured rates of oviposition for different food regimes for young females of *Amblyseius potentillae*. The relative rate of gut emptying is estimated by fitting its value in the model such to obtain an oviposition rate of 0.85 (or 2.26) eggs per day at an average level of 95% gut filling.

Temperature (°C)	Coloration of the the gut[a] (expressed in colour units ranging from 0-7)	Measured rate of oviposition[a] (eggs/day)	Simulated rate of oviposition (eggs/day)
15	1.2	0.16	0.00
	2.0	0.12	0.08
	3.1	0.26	0.22
	4.0	0.27	0.35
	5.0	0.49	0.49
	5.9	0.68	0.66
	6.8	1.00	0.85
25	1.2	0.00	0.00
	2.0	0.64	0.22
	3.0	0.83	0.56
	3.9	1.16	1.00
	5.0	1.33	1.47
	6.0	1.65	1.90
	6.8	2.25	2.26

a. Data from Rabbinge (1976).

the functional response at the given prey densities (Table 36). Both model and experiment indicate the adjustment of the rate of oviposition to the new food level within one day. The initially larger reproduction rate after the change from high to low egg density will therefore be caused by the presence of the gut stores and by the eggs already developed near to oviposition. Similar but opposite reasons apply to the oviposition response after a change from low to high egg density. In another series of experiments the above assumption was tested by measurement and simulation of the time required to resume egg production after different periods of food deprivation. The results, presented in Table 37, demonstrate that the female predator has to recover from the deleterious effects of severe starvation (3 days food deprivation at T = 25°C) before egg production was restarted. A similar conclusion was drawn by Blommers (1977) for *Amblyseius bibens*. Therefore simulation on basis of the assumptions discussed above is only valid for shorter periods of starvation.

Table 35. Simulated and measured rates of oviposition at different prey egg densities for young females of *Metaseiulus occidentalis*.

Prey density (eggs/cm²)[a]	Measured rate of oviposition[a] (eggs/day)	Simulated rate of oviposition (eggs/day)
0.2	0.1	0.1
0.4	0.4	0.4
0.8	0.9	1.0
5.0	2.3	2.5
10.0	3.2	3.3
20.0	3.4	3.5
30.0	3.5	3.6

a. Data from Kuchlein (personal communication); T = 25-27°C; leaf area = 5 cm²; daily replacement of eggs consumed. The rate of predation was not measured in the same experiment but in a similar experiment by Kuchlein, presented in Table 57.

Table 36. The oviposition response of *Metaseiulus occidentalis* to sudden changes in prey egg density.

Female age (in days) starting from final moult	Prey egg density[a] (eggs/cm²)	Measured rate of oviposition[a] (eggs/day)	Simulated rate of oviposition (eggs/day)
3	10.0	3.3	3.3
4	10.0	2.6	3.4
5	10.0	3.0	3.3
6	0.4	1.7	1.5
7	0.4	0.4	0.6
8	0.4	0.5	0.5
9	0.4	0.55	0.4
10	0.4	0.3	0.4
11	0.4	0.4	0.4
12	0.4	0.3	0.4
13	10.0	1.3	1.5
14	10.0	3.2	3.3
15	10.0	3.2	3.3
16	10.0	3.1	3.3

a. Unpublished data from Kuchlein; T = 25-27°C; leaf area = 5 cm²; daily replacement of the prey eggs consumed.

Table 37. The time required for the production of the first egg after different periods of food deprivation. T = 25°C; high density of prey eggs.

Predator species	Period of food deprivation (days)	Time required for the production of the first egg (hours)		
		n	measured	simulated
Phytoseiulus persimilis	0	30	6.2	6.2
	1	30	11.3	10.7
	3	30	13.5	14.2
	6	16	18.2	15.4
Metaseiulus occidentalis	0	15	6.3	6.0
	1	15	9.4	7.9
	3	30	18.6	10.9
	6	15	27.2	11.7
Amblyseius bibens[a]	0	33	6.3	6.0
	2	29	12	10.2
	4	26	12-24	11.4
	6	15	12-24	11.8

a. Data from Blommers (1977).

Comparison of the data obtained on RRGE (or RRA) values with those given in literature reveals many discrepancies. A closer examination is needed, therefore, of the methods adopted by the different authors (Fransz, 1974; Rabbinge, 1976). Fransz estimated RRGE by a fitting procedure related to the observed predatory behaviour, instead of to the conversion physiology. He simulated the predatory activities in a part of his behavioural observations using the relations between the food content of the gut and the behavioural components estimated from the other part of the observations, selecting some starting value for the gut emptying constant. This procedure was repeated until a value of RRGE was obtained that enabled prediction of the behaviour in one part of the observations on the basis of the behaviour observed in the other part. Such a procedure does not, however, guarantee a correct estimation of RRGE, because there may be more than one solution.

Rabbinge applied a more direct method based on the prey-induced gut coloration of *Amblyseius potentillae*, the coloration being visible through its transparant body wall. The coloration is brought about by carotenoids present in the haemolymph of the spider mite; it is correlated with the rate of predation. Although Rabbinge introduced coloration merely as a predation-correlated state variable, it may give an estimate of the relative rate of gut emptying (RRGE). However, it is questionable whether the rate of absorption of other metabolically more important food elements, like proteins, lipids and sugars, equal to that of the carotenoids. Anyway, the results obtained by Rabbinge and Fransz (Table 33) differ largely from those of this report.

3.1.3 Nutritive quality of the prey stages

There is some evidence that food quality depends on the developmental stage of the prey consumed. Because 60-70% of the ingested food is utilized in the production of egg mass, effects of food quality may be determined from the rate of reproduction of a particular prey stage, i.e. in a prey monoculture. However these kind of experiments are difficult to interpret when the prey stages have no equal capture probability, which is due to prey-stage preference of the predator or the escaping capacities of the prey stages. In other words, egg production may be lowered merely by a decrease in the food weight consumed, instead of prey-stage food quality. As will be shown in Subsection 3.2.7, adult female prey run much less risk at being captured than any other stage. Especially this prey stage gives rise to a lower rate of reproduction when offered abundantly in monoculture (*Metaseiulus occidentalis*: Croft & McMurtry, 1972; Croft, 1972; Pruszynski & Cone, 1973) (*Phytoseiulus persimilis*: Shehata, 1973; Begljarow & Hlopceva, 1965). Therefore, to analyse whether the low rate of reproduction is due to a low rate of predation or to nutritive quality, measurements of predation in monocultures of prey stages can be supplied to the model presented in Appendix A and subsequently the reproduction of the predator can be simulated assuming that 1 μg of food ingested from any prey stage has the same nutritive quality as 1 μg egg mass. In this way indications were found that spider mite females as prey give rise to a lower rate of reproduction mainly because they are captured less easily and hence consumed less frequently.

Another approach is to compare reproduction rates in high density monocultures of different prey stages that have been measured at similar rates of predation. For example, Croft & McMurtry (1972) used *Metaseiulus occidentalis* and measured a rate of predation of about 10 prey per day for both egg monocultures and nymph-male cultures, while the appropriate rates of reproduction had a ratio of 3:2. Similarly, Blommers (1976) used *Amblyseius bibens* and measured corresponding rates of predation for eggs and males, while the matching reproduction had a ratio of 4:3. Pruszynski & Cone (1973) used *Metaseiulus occidentalis* and measured a higher rate of predation on eggs then on nymphs. However the rates of reproduction were equal or even higher in case of nymphs as food.

Of course, under more natural conditions of population growth the age distribution of the prey mites will never resemble the extreme of a monoculture of a specific age group of the mites. Although the proportions of the different age groups in the population are rather variable, there is always a mixture of young and old stages due to the continuous reproductive effort of the adult females. The author's experiments indicate that even slight supplies of eggs to monocultures of preovipositional females resulted in a maximal rate of reproduction; addition of 10 eggs to 30 postoviposition females on a leaf disc of 5 cm^2 raised the reproduction of *Metaseiulus occidentalis* from 2.7 eggs per day to 3.6 eggs per day (n = 18, T = 27°C). Shehata (1973) found similar results for *Phytoseiulus persimilis*. Therefore food quality is not considered in the models presented.

3.2 RATE OF SUCCESSFUL ENCOUNTER

In the previous section (3.1), methods to quantify the dynamics of the food content of the gut were discussed. In this section the behavioural components, such as walking, resting, attacking and feeding, are described in relation to the food content of the gut. These components are measured during continuous observations of the predatory behaviour and subsequently related to the food content of the gut as computed from the rate of gut emptying (Subsection 3.1.2) and the observed time series of ingestions. At the start of the experiments female predators are introduced that are standardized with respect to age (3-10 days), feeding history and adaptation to the experimental arena (6 hours). The computation of the state dependent rate of successful encounter is given by the following formula for the total time spent per successful encounter in searching, handling and feeding:

$$\frac{1}{RSE} = FT + \frac{1}{(RE \cdot COIN \cdot SR)}$$

RSE = rate of successful encounter ($time^{-1}$)
FT = feeding and handling time (time)
RE = rate of encounter ($time^{-1}$)
COIN = coincidence in the webbed space (%)
SR = success ratio (%)

The rate of encounter of a predator with its prey is determined by the prey detection distance (Subsections 3.2.1 and 3.2.3) and the walking speed of both predator and prey (Subsection 3.2.2). Assuming that the walking directions of the mites are mutually independent, Skellam (1958) derived the following formula:

$$RE = 2 \cdot d \cdot v \cdot D_{prey}$$

where: D is the symbol for density (number/cm^2) and d for the distance of prey detection (cm); v (cm/time unit) is the resultant velocity of the speed vectors of predator and prey and it is given by:

$$v^2 = v^2_{prey} + v^2_{predator} - 2 \cdot v_{prey} \cdot v_{predator} \cdot \cos \theta$$

θ represents the angle between the momentary directions of predator and prey. Taking expectations we get:

$$Ev^2 = Ev^2_{prey} + Ev^2_{predator}, \text{ since } \int_0^{2\pi} \cos\theta = 0$$

Mori & Chant (1966) suggest the absence of any form of remote sensing in phytoseiid predators. However, it may be that the web threads influence searching by acting as a warning signal for the prey or by drawing the attention of the predator to active prey. These hypotheses are tested in Subsections 3.2.1 and 3.2.3 by comparing the results of an actual experiment concerning the rate of encounter and a calculation of this rate by means of Skellam's formula, where the prey detection distance is taken to be equal to the sum of the radii of the circumferences of prey and predator.

Within a prey colony the phytoseiid predators display a very tortuous walking pattern. This may have two consequences. The rate of encounter may be depressed by revisiting areas already exploited. On the other hand, the residence time of the predator in a prey colony may be increased by this behaviour; for the opposite case, a straight path, a shorter residence time will occur, provided the predator does not turn when arriving at the edge of the colony. The analysis of both the 'recrossing' phenomenon and the factors involved in the residence time is carried out by observation and simulation of the walking behaviour (Subsection 3.2.4 and Section 3.4).

The rate of encounter is also determined by the walking activity of the mites (Subsection 3.2.5). It is defined as the percentage of the observation time that the mite spends walking. Assuming that the activity of both predator and prey is independent of the momentary activity of their neighbouring mites, the rate of encounter can be computed by adding its sub-estimates that pertain to three combinations of predator and prey activity (walk - walk, walk - rest, rest - walk):

$$RRE_{WW} = 2\cdot(r_{prey} + r_{pred}) \cdot \sqrt{v^2_{prey} + v^2_{pred}} \cdot act_{prey} \cdot act_{pred}$$

$$RRE_{WR} = 2\cdot(r_{prey} + r_{pred}) \cdot v_{pred} \cdot (1-act_{prey}) \cdot act_{pred}$$

$$RRE_{RW} = 2\cdot(r_{prey} + r_{pred}) \cdot v_{prey} \cdot act_{prey} \cdot (1-act_{pred})$$

$$RE = (RRE_{WW} + RRE_{WR} + RRE_{RW}) \cdot D_{prey}$$

RRE = relative rate of encounter (RE/D_{prey})
r = radius of the circumference of a mite (cm)
act = activity (%)

The formula of Skellam presented here is restricted to the case of a homogeneous and two-dimensional surface. It can be easily extended to a three-dimensional space, as in the web. However the distribution of the mites and their walking behaviour in the heterogeneous web structure is such that the probability of a visit is not the same for every location in the vertical plane of the webbed space. Therefore the coincidence in space (Subsection 3.2.6) is introduced as a factor, which accounts for the phenomenon that predator and prey may pass over and under each other. In this way the potential number of encounters on a two-dimensional leaf surface is corrected to obtain the number of real contacts in the webbing.

Not all encounters result in predation. The greater and stronger the prey stage, the more difficult it is for the predator to capture the prey. Moreover, the motivational state of the predator, as indicated by the food content of its gut, may determine its chances of seizing prey. Therefore the rate of encounter has to be multiplied by the success ratio (Subsection 3.2.7) to obtain an estimate of the rate of successful encounter. Finally the time spent handling and feeding the prey after successful attack (Subsection 3.2.8) has to be supplemented to the time spent searching per successfully captured prey item. In this way the total time spent per successful encounter (1/RSE) is obtained.

3.2.1 Width of the searching path

The circumference of a predatory mite is not fully determined by taking the distance between the tips of the lateral fore and hind projections of the mite. It is also related to behaviour that enlarges the area covered (Fig. 23). In this respect two behavioural components can be distinguished:

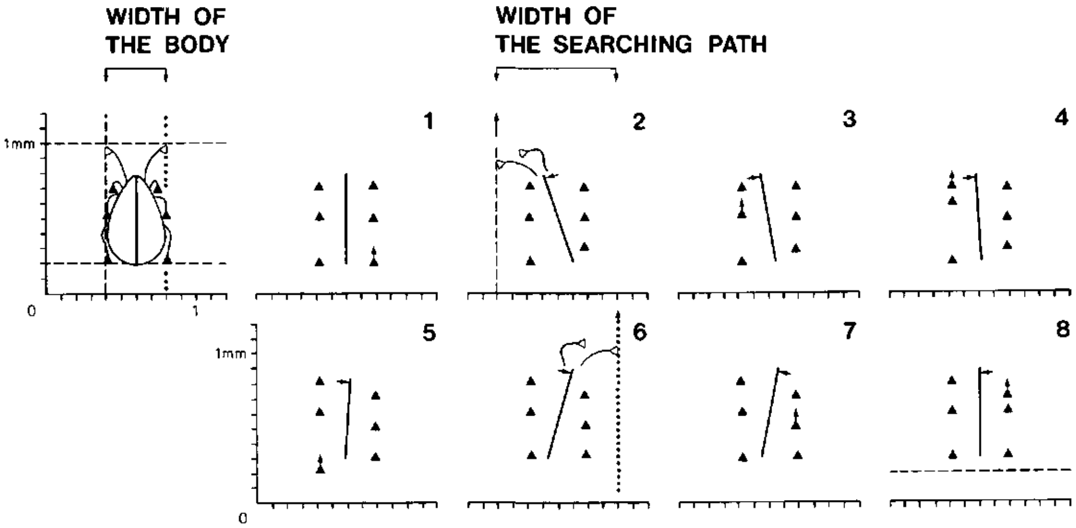


Fig. 23. Width of the searching path determined by body and front leg-movements of a phytoseiid predator. ▲, tarsi of legs 2, 3 and 4; Δ, tarsus of leg 1; arrows indicate leg-movement; straight line represents position of body-axis. Eight successive phases of forward locomotion are given.

first, the frequent turning of the body from one side to the other; second, a superimposed fast ambushing with the front legs, resembling the use of antennae in hymenopterous parasitic wasps. To measure these actions separately a video equipment (camera, recorder and monitor), connected to a binocular microscope, was used, thus offering the facility to fix the moving image.

The observations indicated that an increase of the walking speed results in a decrease of the lateral reach of the predatory female. When the predator is disturbed by something the walking speed is relatively high (Subsection 3.2.2) and the lateral reach almost equals the breadth of a resting mite. In a state of complete rest the front legs are drawn up close to its mouthparts, which causes the length to be equal to the length of the soma. Spider mites, with their rigid shuffling way of walking, do not show any of these characteristics.

The measurements of the lateral and distal reach of undisturbed female predators in different states of activity are presented in Table 38. Those of the spider mites are given in Table 39, related to the developmental stage. It may be concluded that except for the resting state of the predators, the breadth of the mites is very near to their length, so that it is not unrealistic for simulation purposes to conceive mites as circular units with a diameter equal to half the sum of the real length and breadth. These measurements will be used in calculations with Skellam's formula for the rate of encounter, for which the distance of prey detection is assumed to be equal to the sum of the radii of predator and prey (Subsection 3.2.3).

Table 38. The lateral reach and the distal length of the females of four phytoseiid species (n = 20).

Predator species	State	Length (mm)		Breadth (mm)		Diameter (mm)
		$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	(length + breadth)/2
Phytoseiulus persimilis	walking	0.98	0.147	0.84	0.068	0.91
	resting	0.71	0.040	0.42	0.020	0.565
Amblyseius potentillae	walking	0.81	0.038	0.71	0.040	0.76
	resting	0.69	0.034	0.43	0.027	0.56
Amblyseius bibens	walking	0.65	0.037	0.56	0.020	0.605
	resting	0.62	0.030	0.30	0.029	0.46
Metaseiulus occidentalis	walking	0.62	0.033	0.52	0.018	0.57
	resting	0.62	0.031	0.27	0.028	0.445

Table 39. Length and breadth of the developmental stages of *Tetranychus urticae* (n = 10).

Developmental stage	Length (mm)		Breadth (mm)		Diameter (mm)
	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	(length + breadth)/2
egg	0.137	0.007	0.137	0.007	0.137
larva	0.307	0.017	0.219	0.017	0.263
protonymph	0.411	0.040	0.272	0.035	0.342
deutonymph ♀	0.539	0.040	0.362	0.048	0.451
male	0.592	0.032	0.376	0.044	0.484
preoviposition female	0.749	0.077	0.443	0.082	0.596
oviposition female	0.779	0.061	0.534	0.061	0.657

3.2.2 Walking velocity

The walking velocity was measured as the displacement along the track per unit of time. These walking tracks were registered with the video equipment shown in Fig. 24. This experimental set up provided an almost perpendicular projection of the paths with a magnification of about 8 times. Although the experimental leaves were selected on their flatness, the walking tracks near to the edge of the leaf were incorrectly projected on the screen due to the curvation of the leaf and therefore discarded. To prevent any possible orientation by the mites on a surrounding unequal light distribution, the experimental leaf was enclosed in an 'opal' Perspex cylinder, which diffused the lateral incoming light. The light distribution was measured with a selenium unit connected to an ampère-meter. The radiation flux varied between 2 and 2.3 Watt per m^2 near the leaf.

The walking time was measured simultaneously by means of a stop watch; each 10 second period was marked on the drawings of the walking paths. The walking activity of the mites was frequently interrupted by short or long stops. Those stops that lasted less than 1 second could not be separated by observers from the walking-time registration due to lags in reaction time. From these measurements of walking time and displacement, the mean walking speed was computed. An attempt was also made to characterize the variation in walking speed by computing the variance of the velocities in the arbitrary 10-second periods.

The walking velocity was studied in relation to the period of food deprivation, temperature, webbing and the side of the leaf. To study these relations it was very important to distinguish between edge-oriented walks and walking paths on the leaf surface. The edge-oriented walking becomes apparent by intensive inspection of leaf-edge-related structures and the regular

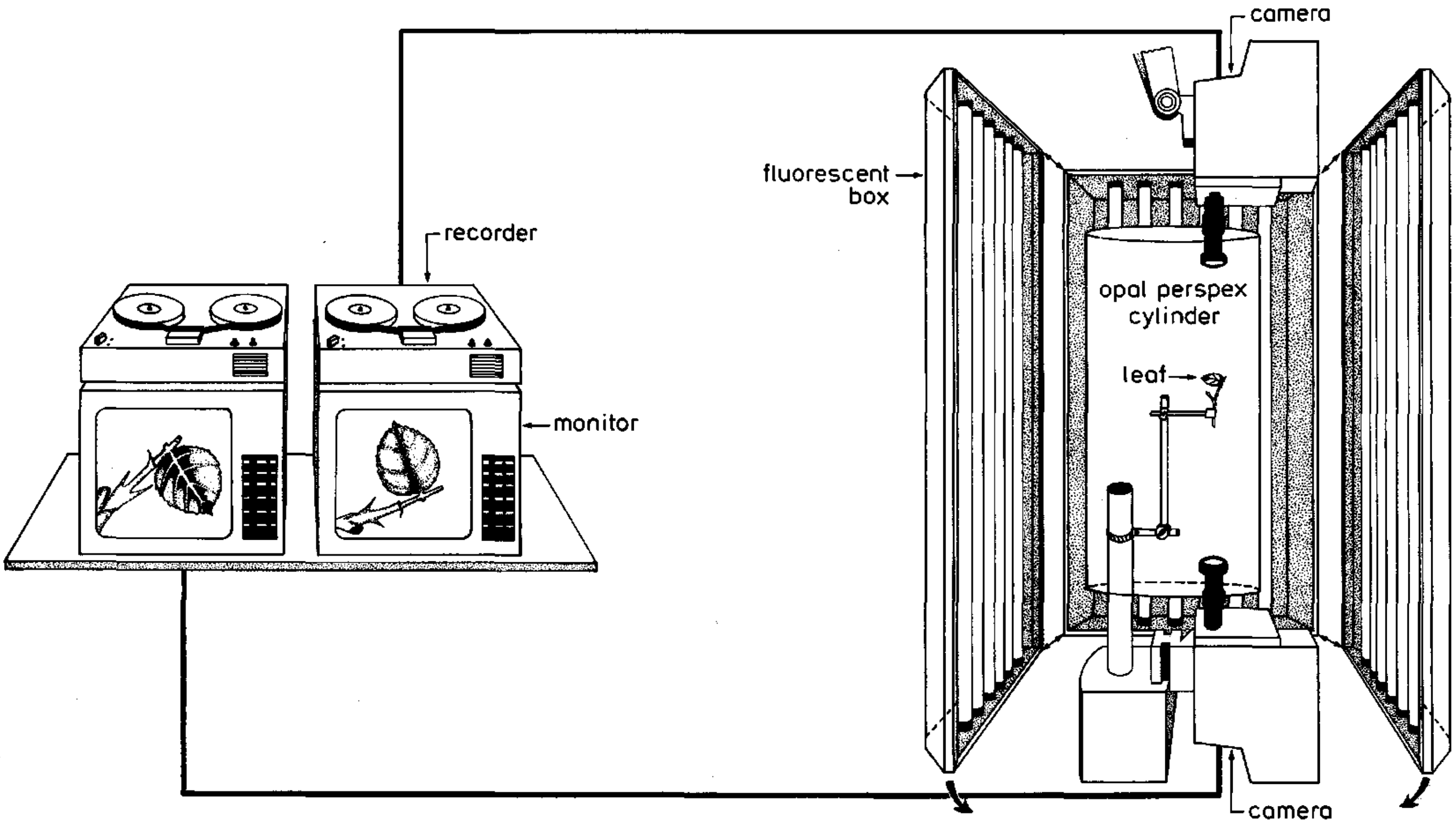


Fig. 24. Video equipment for registering walking paths of the mites.

Table 40. The walking velocity of females of four phytoseiid species in relation to starvation, temperature, side of the leaf and webbing.

Predator species	Factor manipulated	Walking velocity on leaf without webbing (mm/s)[a]				Walking velocity on leaf with webbing (mm/s)[a]			
		upperside		underside		upperside		underside	
		$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$
Phytoseiulus persimilis	starvation period								
	0 days (T = 20°C)	1.16	0.11	0.25	0.04	0.19	0.05	0.18	0.03
	1 day	1.21	0.15	-	-	0.20	0.02	0.18	0.02
	2 days	1.36	0.22	-	-	-	-	-	-
	disturbance by a touch with a brush	2.35	-	-	-	-	-	-	-
	temperature								
	15°C	1.11	0.12	-	-	0.19	0.02	-	-
	29°C	1.48	0.14	-	-	0.21	0.01	-	-
Amblyseius potentillae	starvation period								
	0 days (T = 20°C)	0.68	0.22	0.21	0.05	0.16	0.03	0.17	0.04
	1 day	0.85	0.22	0.24	0.03	-	-	-	-
	2 days	0.92	0.26	0.23	0.04	-	-	-	-
	disturbance by a touch with a brush	1.82	0.34	-	-	-	-	-	-
	temperature								
	15°C	0.59	0.16	-	-	0.14	0.02	-	-
	29°C	0.69	0.17	-	-	0.16	0.02	-	-

Metaseiulus occidentalis	starvation period								
	0 days (T = 20°C)	0.66[b]	0.04	0.26	0.02	0.18	0.01	0.17	0.02
	1 day	0.65	0.06	0.27	0.03	-	-	-	-
	2 days	0.69	0.06	-	-	-	-	-	-
	disturbance by a touch with a brush	0.78	-	-	-	-	-	-	-
	temperature								
	15°C	0.64	0.03	-	-	0.17	0.02	-	-
	29°C	0.73	0.07	-	-	0.18	0.02	-	-
Amblyseius bibens	starvation period								
	0 hours (T = 20°C)	0.55	-	-	-	0.22	-	-	-
	6 hours	0.50	-	-	-	0.20	-	-	-
	8 hours	0.70	-	-	-	0.23	-	-	-
	12 hours	0.92	-	-	-	0.43	-	-	-
	18 hours	0.50	-	-	-	0.35	-	-	-
	28 hours	0.47	-	-	-	0.30	-	-	-

a. Number of individual mites used per treatment varied from 8 to 12, each being observed for 3-8 minutes walking time.

b. Kuchlein (to be published) measured a walking velocity of 0.47 mm/s on leaf discs of the Lima bean (T = 27°C).

return of the mite towards the leaf edge after loosing contact with it. A few times the mites lost contact with the edge and did not return. On those occasions they were swaying to and fro; to the author they appeared to be disoriented. Only the walking paths on the leaf surface, i.e. not edge-oriented, are used in the treatment of walking velocity. The edge-oriented walk will be discussed in relation to the time spent outside the prey aggregations (Part 2).

The walking behaviour can be strongly influenced by experimental manipulation. For example, disturbances can be observed after the predatory might are displaced by a brush. To illustrate the effect on the walking speed some measurements were made of the walking behaviour of disturbed predators; these are given in Table 40. Disturbance diminishes within two hours. Therefore the behavioural observations of predators were used only after a resting period of some length (> 5 min.), so that the predator started walking spontaneously.

The effect of the starvation period on the walking speed of the predators is probably rather complicated (Table 40). When starved for two consecutive periods of a whole day, the walking speed of all four phytoseiid species studied increased by less than 30%. However, when *Amblyseius bibens* was starved for periods of less than 1 day, the walking speed initially increased, subsequently followed by a decrease. The latter effect was also measured by Sandness & McMurtry (1972) for *Amblyseius largoensis*. Kuchlein (to be published) found indirect evidence for an increase in walking velocity/activity for the case of *Metaseiulus occidentalis* at low densities of the prey (from 3 eggs per 5 cm^2 to 1 egg per 10 cm^2).

The effect of temperature on the displacement of female phytoseiids (= observation time × walking speed × fraction of the observation time spent walking) was studied by Everson (1979) and Penman & Chapman (1980). Everson concluded, that the displacement of *Phytoseiulus persimilis* was not influenced by temperature on both a glass substrate and a bean leaf. Penman & Chapman obtained similar evidence for *Metaseiulus occidentalis* in the range of 15-30°C (relative humidity = 75%), but below 15°C displacement was clearly decreased. This result was also obtained by these authors for the case of *Tetranychus urticae*. The results of the present study (Table 40) indicate a small or no increase of the walking speed of the predators at temperatures increasing from 15°C to 30°C. According to Penman & Chapman (1980) the humidity level is of minor importance for the displacement of females of *Metaseiulus occidentalis* and *Tetranychus urticae*.

Although temperature did exert some influence on the walking velocity of the predators, its effect was minor compared to that of the structure and position of the substrate. The walking speed of the four phytoseiid species studied was reduced to 15-30% as a consequence of their position on the downward-facing side of the leaf. Turning experiments with the experimental leaf showed that this result was not caused by the texture differences be-

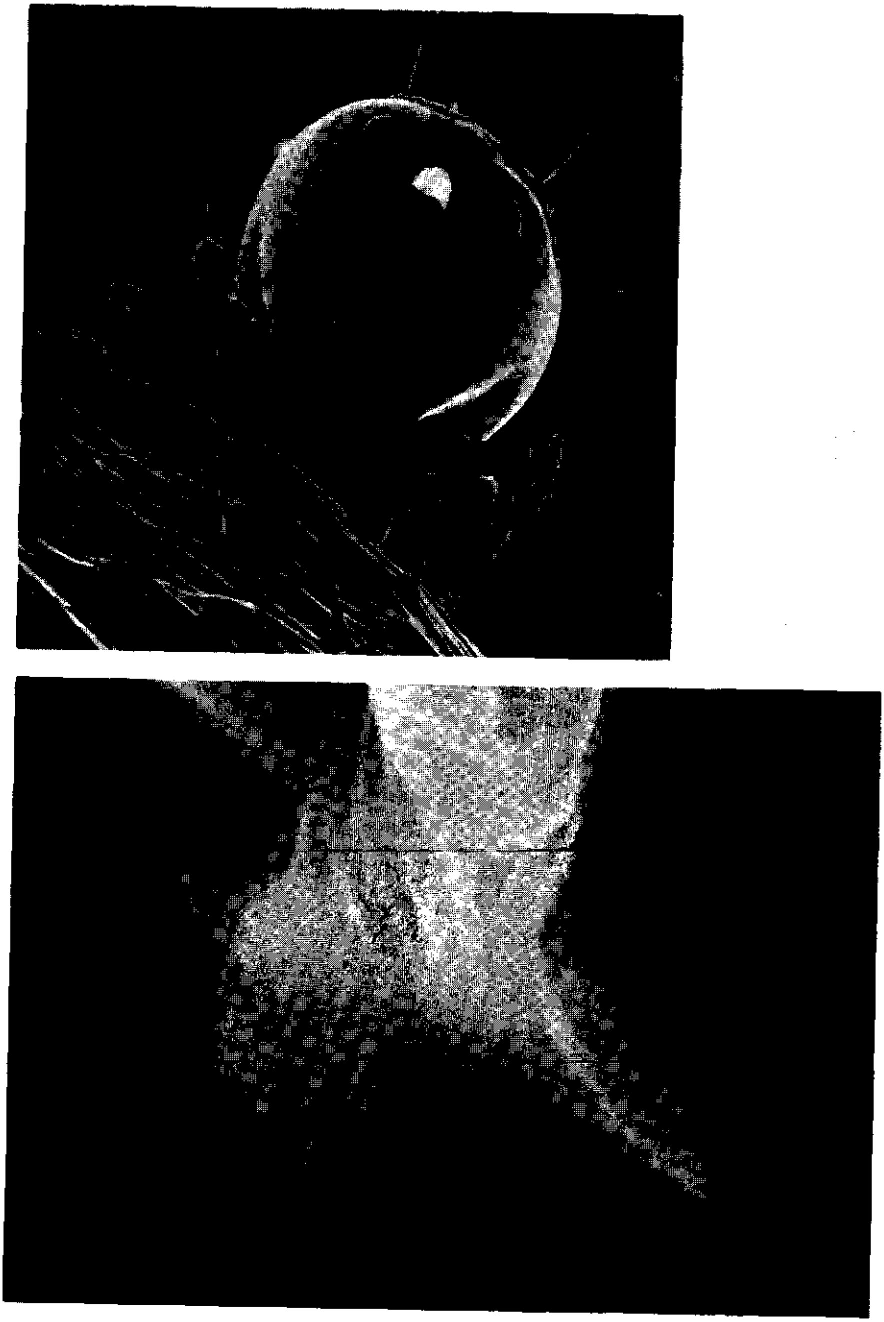


Fig. 25. A. Back view of a female predator (*Amblyseius potentillae*) resting next to a leaf mid-rib (magnification: 90 ×). *B.* Detail of the tarsus of the hindleg (magnification: 6000 ×) shown in A. Notice the position of the claws and the swab-like empodium and compare with the position of the claw remnants and the empodial hairs of the spider mites, shown in Figure 26.

tween the upper and lower cuticle, but probably by gravitational force. This phenomenon may be related to the adhesive properties of the swab-like empodium and the claws of phytoseiid mites (Fig. 25), because their walking speed was not reduced when walking on the mid-rib of the downward-facing side of the rose leaf. The walking speed of the spider mites was not influenced by the position of the leaf, possibly because they are always attached to the leaf, as web threads are continuously produced during walking (Saito, 1977a). Artificial trembling of the leaf caused the spider mites and the predators to lose contact with the leaf surface, but it was often observed that the two-spotted spider mites crawled along its web thread up to the surface after this manipulation.

Both spider mites and predatory mites walked more slowly in a webbed environment (Tables 40 and 41) if compared with their walking velocity on the upward-facing side of the rose leaf. Even a very low webbing density caused the predatory mites to slow down. The web structures were inspected intensively with their front legs. Once a passage through these structures was detected a forward movement was made. Presumably the long dorsal setae pointing backwards on the pear shaped phytoseiid body serve as a wedge in the sticky web during forward locomotion. Sandness & McMurtry (1972) reported that the stickiness and the physical presence of several strands of webbing impeded the progress of *Amblyseius largoensis*. In the present study it was observed a few times that females of *Amblyseius potentillae* stuck to the web with their dorsal plate. An explanation for this fact could be found in the absence of long setae on the dorsum of *Amblyseius potentillae*, the longer setae being positioned near the edge of the dorsal plate. It may be worthwhile to reconsider acarine predator-prey relations from this point of view. When mites are in the webbing the influence of gravity can be neglected. Likewise, the effect of temperature on the walking velocity was not significant for mites moving in the webbing. Surprisingly the same rule applies to the interspecific differences. This implies that the walking velocity is not responsible for any interspecific difference in the intra-colony rate of predation, but it may be relevant in the specific capacity of inter-colony dispersal (Part 2).

3.2.3 Distance of prey detection

As stated by Mori & Chant (1966), initial contact of *Phytoseiulus persimilis* with its prey appears to be matter of chance. The prey mites are apparently first detected by contact with the anterior tarsi of the front legs, which are extended in front of the body. After contact the predator usually moves closer to the prey and palpates it with its pedipalps before penetrating the mite's soma. On the basis of behavioural observations and scanning electron micrographs of the setae on the pedipalps and the anterior tarsi of legs I Jackson (1973, 1974) suggests that mechanoreception and con-

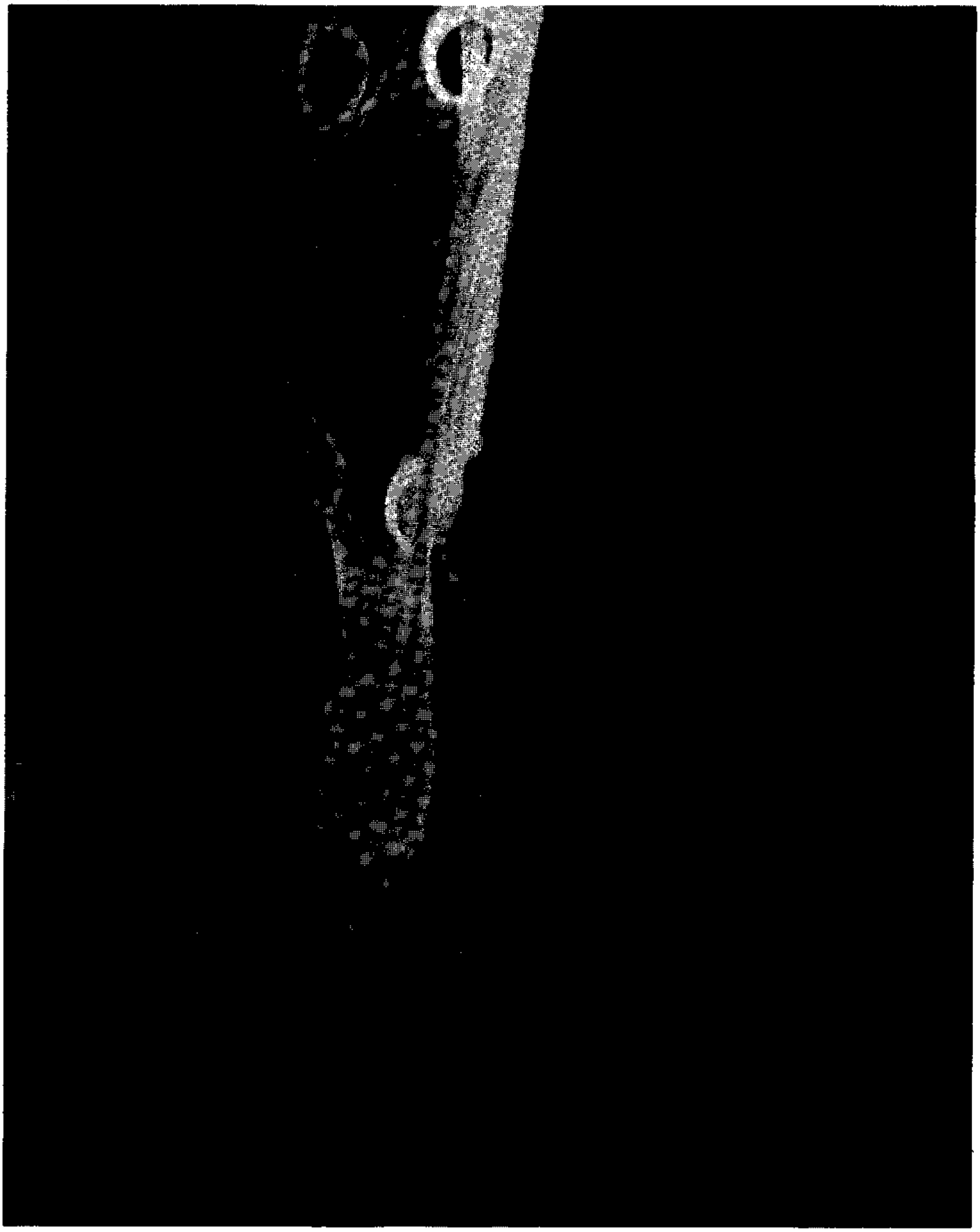


Fig. 26. Tarsus of a male of *Tetranychus urticae* (magnification: 6000 ×). Notice the position of the empodial hairs *on* the webbing strand and the position of the four claw remnants (τετρα ονυχοι, four fingers) *aside* of this strand.

Table 41. The walking velocity of different developmental stages of *Tetranychus urticae* (T = 20°C).

Developmental stage	Walking velocity on leaf without webbing (mm/s)				Walking velocity on leaf with webbing (mm/s)			
	upperside		underside		upperside		underside	
	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$
larva	0.08	0.01	0.11	-	-	-	0.05	-
protonymph	0.18	-	0.10	-	-	-	-	-
deutonymph female	0.39	-	0.28	-	-	-	-	-
male	0.63	0.18	0.51	0.17	-	-	0.22	0.05
preoviposition female	0.92	0.28	0.80	0.24	-	-	-	-
oviposition female	0.23	0.05	0.18	0.04	0.11	-	0.10	0.03

NB. Number of individual mites used per treatment varied from 11-15, each being observed for 4-8 minutes walking time.

tact chemoreception is involved at both tarsal and palpal contact with the prey.

However web may interfere with searching by providing a warning signal to the prey or by drawing the attention of the predator to active prey. Therefore a distinct validation of Skellam's model is needed. To accomplish this, estimates of the rate of encounter were compared with the results of an experiment where the encounters between predator and prey were scored on a time scale. Hungry predators (0.5 days food deprivation, T = 20°C) were used to ensure reaction to the presence of prey, if any. The experiments were made in the presence and absence of web. The effect of the mobility of the prey was also investigated, using eggs and females of *Tetranychus urti-*

Table 42. Measured and simulated rates of encounter between female phytoseiid predators and a mobile (female) or immobile (egg) stage of *Tetranychus urticae* in absence or presence of webbing.

Predator species	Prey stage and density	Webbing	Rate of encounter (number/min)		Total observation time (min)
			simulated	measured	
Phytoseiulus persimilis	4 eggs per cm^2	absent	3.26	3.35	32
Amblyseius potentillae	36 eggs per cm^2	absent	16.3	18.9	21
	2 eggs per cm^2	absent	0.91	1.08	96
	0.25 eggs per cm^2	absent	0.12	0.14	160
Metaseiulus occidentalis	4 egss per cm^2	absent	1.13	1.10	86
Phytoseiulus persimilis	4 egss per cm^2	present	0.47	0.57	222
Amblyseius potentillae	4 eggs per cm^2	present	0.32	0.36	245
Metaseiulus occidentalis	4 eggs per cm^2	present	0.30	0.34	250
Phytoseiulus persimilis	10 ♀[a] per cm^2	present	1.76	1.73	92
Amblyseius potentillae	10 ♀[a] per cm^2	present	1.37	1.24	110
Metaseiulus occidentalis	10 ♀[a] per cm^2	present	1.34	1.25	82

a. The walking activity of the female spider mite = 4%.

cae as prey. The activity of the female spider mite was registered and accounted for in the calculation of the rate of encounter. The female predators, however, were only observed when they were active. Care was taken that the mites were accustomed to the experimental leaf, which was placed on wet cotton wool to keep the leaf fresh and prevent the mites from leaving the leaf surface. The arena was marked by a square on the ocular of a binocular microscope. It was smaller than the rose leaf to avoid any edge effect. Therein the eggs (immobile category) were spread equidistantly. In this way unnecessary variation in the results as a consequence of the casual occurrence of clusters of eggs were prevented. For the mobile female prey this was obviously not possible. The projection of the ocular square on the leaf surface resulted in an imaginary arena of 4 cm^2. A female predator was allowed to traverse this arena and the number of contacts during the time spent in the arena were scored. On a webbed substrate encounters were also scored when the projections of prey and predator on the horizontal leaf plane overlapped. The mean rate of encounter was calculated as the total number of encounters scored divided by the cumulative time spent walking in the arena.

In Table 42 the measured rates of encounter are given together with the estimates according to Skellam's formula. From these results it can be concluded that the contribution of olfaction or web (= the difference between the measured and the calculated rate) was always less than 20% of the calculated rate. For eggs as prey, all differences between simulation and measurement disappear when the diameter of the simulated egg is doubled. This suggests that the eggs are scented from near by. In case the prey is a mobile female, the measured rate turns out to be consistently smaller than the calculated rate. An explanation for this small but consistent difference may be found in the warning action of web vibrations caused by the predator.

The overall conclusion is that the influence of olfactory or other stimuli emerging from the web is low, so that it is allowed to use the formula of Skellam for the calculation of the rate of encounter. This means that predatory preference for a prey stage or the escaping capacity of the prey may for computational purposes be considered to arise at the moment of contact.

3.2.4 Walking pattern

The walking pattern of the predator affects the rate of encounter with prey in two ways. In the first place it determines the time spent in a prey colony. When the edge of the colony does not influence the walking behaviour of the predator, a straight path causes the residence time to be minimal and the distance between starting and momentary position (= linear displacement) to be maximal. The more tortuous the walking behaviour, the smaller the linear displacement and thus the longer the residence time of the predator in a prey colony. Of course, the transition of colonized leaf surface to uncolonized parts of the plant may induce the return of a predator when it arrives at this edge. However, such a mechanism has not been reported so far with respect to Phytoseiidae.

In the second place, a very tortuous walking pattern may cause a depression of the rate of encounter if the predator devours the prey items encountered; the predator may stay too long on a spot previously occupied by devoured prey. Predatory mites walk tortuously when searching in webbing (Fig. 27). Therefore, the walking paths being available from the measurements of the walking velocity (Subsection 3.2.2), it was worthwhile to analyse the effect of the walking pattern on the residence time of a predator in a prey colony and on the rate of encounter between predator and prey. For this purpose a simulation model of the walking behaviour was constructed.

The walking behaviour of an individual animal can be simulated as follows. Each time interval, which is equal to the quotient of step size and walking velocity, the animal makes a forward movement with a change in direction over a fixed distance. This angular deviation is chosen at random from a distribution of changes in walking direction ($-\pi$, $+\pi$) obtained from the walking paths registered on video equipment. These angular deviations are found in principle by determination of the angle between two successive directions after a linear step of a fixed length (Fig. 28). The shape of the frequency distribution strongly depends on the magnitude of the step. 'Advancing with seven-league boots' the distribution tends to the Gaussian

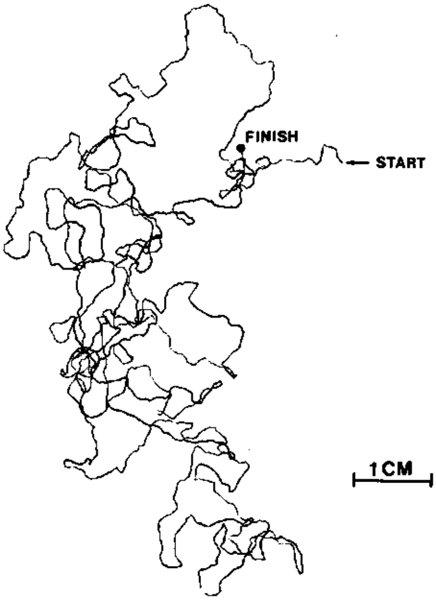


Fig. 27. Walking path of a female predator (*Phytoseiulus persimilis*) on a webbed leaf area.

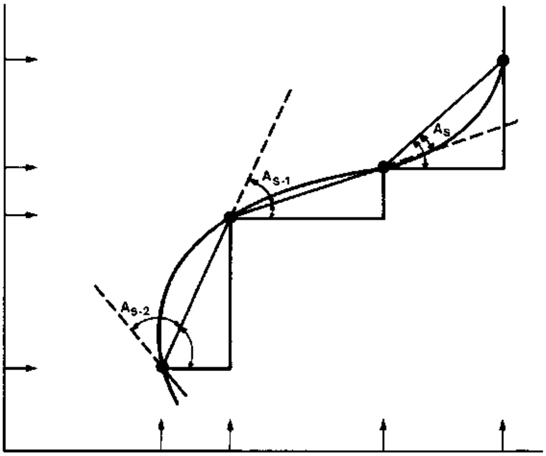


Fig. 28. Determination of three consecutive angular deviations (A_{s-2}, A_{s-1}, A_s) after pacing linear distances of fixed length.

or uniform-type, while for a small step the tendency is towards a Student-type distribution. To justify comparison of different distributions measured and to fulfill the requirements of an accurate description of the walking paths, a step size is selected of half the average length of the mites (= 0.04 cm), which corresponds to about 2 times the step length of adult mites. Correlation between successive changes in walking direction can be accounted for by an auto regression model:

$$A_s = \alpha_1 \cdot A_{s-1} + \alpha_2 \cdot A_{s-2} + \dots\dots\dots\dots + \alpha_m \cdot A_{s-m} + X_s$$

A_s = directional change at step number s
X_s = random process to obtain angular deviations from a frequency distribution, corrected for autocorrelations
$\alpha_1 \ldots \alpha_m$ = autoregressioncoefficients
m = order of the process

The first-order auto regressive process is then:

$$A_s = \alpha_{s-1} \cdot A_{s-1} + X_s$$

The procedures to obtain and to interpret the values of the auto correlation coefficients, to calculate the auto regression coefficients from the auto correlation coefficients, and finally to determine the order of the process are explained in Appendix B.

For comprehensive representation of the results it is useful to describe the frequency distributions by their moments. However, the Gaussian and Student-type distributions proved to be inadequate due to the probability 'mass' located in the tails of the measured distributions. The Tukey distribution was chosen due to its flexibility in this respect. The mathematical form of this inverse, symmetric, continuous and cumulative distribution is:

$$X_s = \mu + \sigma \cdot Y_p$$

$$Y_p = \begin{cases} (p^\lambda - (1-p)^\lambda)/\lambda & \ldots\ldots\ldots\ldots \lambda \neq 0 \\ \ln(p/(1-p)) & \ldots\ldots\ldots\ldots \lambda = 0 \end{cases}$$

μ = mean angular deviation

σ = scale parameter

λ = kurtosis-related parameter

p = cumulative frequency of angular deviations

The flexibility of this three-parameter distribution finds expression in the fact that the kurtosis related value of λ causes the distribution to approximate the shape of some well known distributions:

λ = 1 ...... uniform

λ = 0.14 ...... normal

λ = 0 ...... logistic

λ = -0.85 ...... Student's t_1 or Cauchy

The maximum likelihood procedure for the estimation of μ, σ and λ, plus a test on goodness of fit, are given in Appendix C.

The simulation process is as follows. A change in walking direction (in radians), X_s, is computed for a random p value ($0 < p < 1$) drawn from a uniform distribution. This change in direction is subsequently added to the actual direction, and from the cosine and the sine of this new direction the new x and y positions are obtained, taking the step size as the length of the hypotenuse. In Fig. 29 the relation between the shape of the distribution and its matching walking path are visualized. These simulations demonstrate the influence of the scale and tail length of the frequency distribution on the simulated walking path.

Comparable simulation approaches can be found in Siniff & Jessen (1969), Kitching (1971), Cody (1971, 1974), Jones (1977, 1978), Pyke (1978), Yano (1978), Sirota (1978), Inoue (1978), Waddington (1979) and Baars (1979). Some of these authors have based their frequency distributions on angular deviations after variable time periods, which makes comparison of different distributions essentially impossible. Other authors used angular deviations after fixed time periods, so that their conclusions pertain to both walking velocity and pattern. Pyke (1978) and Jones (1978) noted the possibility that an arthropod has some limited memory concerning the direction of the immediately previous movement. They did not present a model of this particular aspect.

The walking tracks registered by means of the set up discussed in Subsection 3.2.2, were used for the measurement of the frequency distributions of angular deviations. In principle this was done by proceeding along the

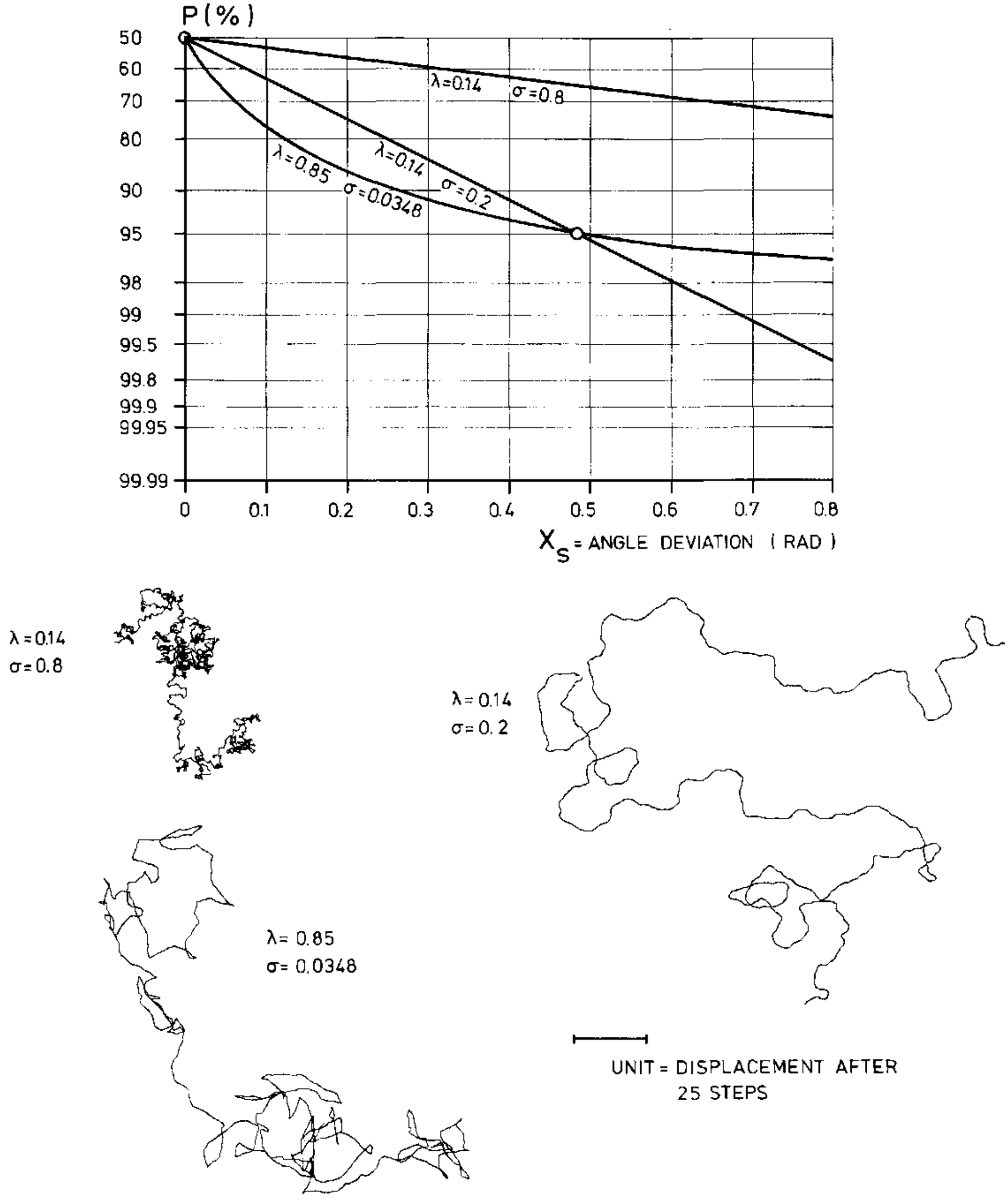


Fig. 29. Relation between the shape of the frequency distribution of angular deviations and the actual walking path. Two differently scaled Gaussian distributions and another distribution with a longer tail are plotted on probability paper of the Gaussian distribution. The matching simulations of walking paths are shown below and the computer program is listed in Appendix D.

track with fixed linear steps and by subsequent determination of the angular deviation between successive directions (Fig. 28). At the end of each path the collected angles were ordered into a frequency distribution ($-\pi$, $+\pi$). This procedure and the subsequent estimation of the Tukey parameters, auto regression and correlation coefficients, plus a final test on the goodness of fit, were executed with the aid of a computer program constructed for this purpose (Ruardij, 1981). The paths can be supplied to the program in the form of a series of x,y coordinates via an x-y tablet connected to the computer. The distances between those coordinates are inevitably subject to irregularities due to human inaccuracy. Therefore an interpolation method (Spline or Aitken-Lagrange) operates in the program to obtain a continuous walking path along which the fixed step size can be paced. Overshoot problems with the interpolation at sharp turns in the walking paths are solved initially by interpolation over smaller parts of the walking track and ultimately by simple linear interpolation. The program was tested in a series of experiments with straight and circular walking paths.

The walking tracks analyzed in this paragraph originate from solitary mites, walking on explicitly defined substrates. If the effect of contact between predator and prey was studied, this was accomplished by putting the prey close to a predator and subsequently removing it after the occurrence of the desired action. To obtain a webbed area without any prey, both males and preovipositional females were put on a fresh leaf, from which they were discarded after about 2 days to prevent egg deposition. The results of the analysis of these walking paths are presented in Tables 43 and 44. To get a better estimation of the correlation between successive angular deviations, only the longest walking paths were used. In most cases the auto correlations showed a low level of correlation, if any. When significant values occurred ($|\alpha_k| > 2/\sqrt{N}$; N = total number of steps), these normally indicated a first-order auto regressive process. The irregular pattern of positive and negative values also supports the conclusion, that the mites do not show an autocorrelated walk. The evaluation of the different treatments is facilitated by tabulating the linear displacement after 200 step units next to the values of the Tukey parameters and the auto correlations. From these displacements it can be concluded that the effect of the starvation period is rather small, even in combination with previous contact with prey. However, the substrate appeared to be very important, as was also the case for the walking velocity. The tortuosity of the walking paths in the webbing is expressed by an increase in the value of the scale parameter σ, which in turn causes the decrease in the estimated linear displacement. The position of the predator on the upper or underside of the leaf does not affect the walking pattern, although the walking speed was severely reduced on the side facing downward. Consequently three regions can be distinguished on the leaf with respect to the walking speed and the walking pattern:

- the upperside of the leaf, the mid-rib on the underside of the leaf and

Table 43. Frequency distribution of angular deviations (rad) and auto correlations for the case of different stages of *Tetranychus urticae*.

Stage	Webbing intensity	Side of the leaf	λ	σ	$P(\chi_n^2>X^2)$[a]	Auto correlation				$2/\sqrt{N}$	Linear displacement (steps)
						k = 1	k = 2	k = 3	k = 4		
larva	-	upper	-0.151	0.263	0.45	-0.029	-0.071	0.111	0.087	0.106	39
		under	-0.254	0.196	0.28	-0.062	-0.037	0.117	0.068	0.133	42
protonymph	-	upper	-0.113	0.262	0.45	0.105	-0.011	0.066	-0.001	0.097	38
		under	-0.101	0.247	0.74	-0.227	-0.017	0.106	0.034	0.166	45
deutonymph	-	upper	-0.343	0.144	0.95	0.168	-0.001	-0.009	-0.010	0.099	46
		under	-0.256	0.175	0.45	0.051	0.049	0.033	-0.084	0.067	47
adult male	-	upper	-0.236	0.130	0.52	-0.148	-0.002	-0.042	0.021	0.065	82
		under	-0.188	0.139	0.40	-0.152	0.010	-0.063	0.019	0.038	81
preoviposition female	-	upper	-0.195	0.174	0.30	-0.015	-0.015	0.050	0.046	0.073	51
		under	-0.107	0.184	0.50	0.011	-0.021	-0.036	-0.058	0.089	64
oviposition female (young)	-	upper	-0.266	0.151	0.75	0.033	0.021	-0.016	-0.022	0.052	53
		under	-0.156	0.150	0.45	-0.120	-0.039	0.023	-0.042	0.060	77
oviposition female (old)	-	upper	-0.084	0.314	0.30	0.043	0.021	-0.072	0.007	0.069	37
		under	-0.015	0.348	0.50	0.093	0.013	-0.066	0.018	0.077	35
adult male	normal	under	-0.179	0.264	0.70	-0.234	-0.165	0.061	0.024	0.118	50
	low	under	-0.193	0.194	0.15	-0.093	0.112	0.004	0.315	0.221	42
adult female	normal	under	-0.190	0.259	0.45	0.116	0.051	0.011	0.001	0.234	35
	low	under	-0.400	0.174	0.33	-0.148	-0.122	-0.154	0.056	0.138	37

a. $P(\chi_n^2>X^2)$ = critical level; X^2 = test statistic; $n = c-1-3$; c = Number of frequency classes; N = Number of steps.

Table 44. Frequency distribution of angular deviations (rad) and auto correlations for the case of young female predatory mites.

Predator species	Time of food deprivation	Webbing intensity	Side of the leaf	λ	σ	$P(\chi_n^2 > X^2)$[a]	Auto correlation (ρ)				$2/\sqrt{N}$	Linear displacement (steps)
							k = 1	k = 2	k = 3	k = 4		
Amblyseius potentillae	0			-0.101	0.165	0.10	-0.119	0.069	-0.026	-0.024	0.078	73
	24			-0.056	0.188	0.40	-0.188	0.097	0.014	-0.048	0.087	71
	48			-0.027	0.233	0.60	-0.164	0.026	0.014	-0.025	0.054	63
	48[b]			-0.058	0.238	0.50	-0.154	0.029	-0.034	-0.018	0.060	60
		normal		0.129	0.566	0.45	0.019	-0.064	-0.018	-0.065	0.094	27
		low		-0.235	0.201	0.80	0.125	-0.154	-0.228	-0.062	0.119	51
	24-28		upper	-0.027	0.233	0.60	-0.164	0.026	0.014	-0.025	0.054	63
	24-28		under	-0.070	0.231	0.15	-0.159	0.029	-0.034	-0.018	0.060	60
Phytoseiulus persimilis	24-28		upper	-0.117	0.13	0.65	-0.161	-0.051	0.031	0.039	0.095	96
	24-28		under	-0.099	0.16	0.60	-0.071	-0.021	0.052	0.062	0.201	72
	0	normal		-0.047	0.301	0.80	0.099	-0.123	-0.136	-0.087	0.084	47
	48	normal		-0.035	0.319	0.85	0.175	-0.154	-0.124	-0.098	0.093	46
Metaseiulus occidentalis	24-28		upper	-0.117	0.21	0.80	0.012	-0.314	-0.115	0.125	0.168	68
	24-28		under	-0.131	0.24	0.80	0.012	-0.222	-0.026	0.098	0.108	43
	0	normal		-0.068	0.271	0.60	0.111	0.052	0.060	0.033	0.119	32
	48	normal		-0.099	0.26	0.50	0.302	0.096	0.112	0.063	0.203	32

a. $P(\chi_n^2 > X^2)$ = critical level; X^2 = test statistic; n = c-1-3; c = number of frequency classes; N = Number of steps.

b. Immediate behaviour of predator upon contact only with prey after 48 hours of starvation.

the stem: fast and straight walk, predominantly edge-oriented

- the underside of the leaf excluding the mid-rib: slow and straight walk
- the webbed area of the leaf: slow and tortuous walk.

Evidently the residence time of the female predator per unit webbed area is promoted relative to that per unit of any other plant area. This tendency becomes even more obvious when the data on walking activity at the above-plant regions (Subsection 3.2.5) are considered.

It may be questioned whether the presence or abundance of prey in the webbed area has an additional arresting effect on the female phytoseiids. For example, several arthropod predators and parasitoids change their walking pattern from straight to tortuous after contact with a prey item, presumably to increase the probability of a subsequent capture of patchily distributed prey (Hassell, 1976, p. 50-55). Besided, the walking speed and walking activity may decrease when predators arrive at local patches of prey. Finally, there may be some patch-specific signal causing the return of the predator when it arrives at the edge of the colony. To elucidate the role of the above factors in the causation of the residence time the walking behaviour is also measured in colonies with prey and experimentally defined residence times are compared with estimates, based on simulations of the walking behaviour, which assume the absence of specific returns of the predator, when arrived at the edge of the colony. Both measurements and simulations are discussed in Subsection 3.4.1.

To give a general idea of the sensitivity of the linear displacement for the parameters of the Tukey distribution and the auto regression coeffi-

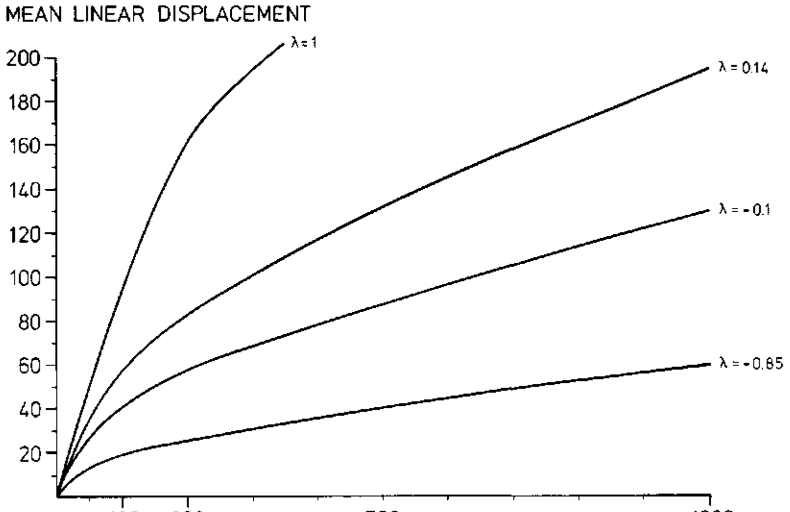


Fig. 30. Mean linear displacement, expressed in step units, in relation to the number of steps moved at different levels of λ ($\sigma = 0.2$).

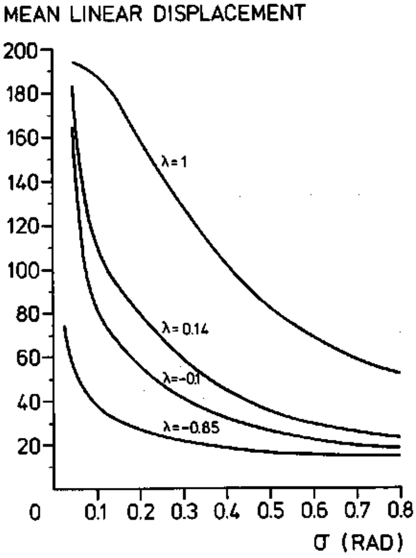


Fig. 31. Mean linear displacement after 200 steps, expressed in step units, in relation to the scale parameter σ at different levels of the shape parameter λ.

cients, three graphs are given based on the mean values of a series of 1000 Monte Carlo simulations. In each graph the mean change in walking direction is chosen to be zero and the values of λ are those of the approximate uniform (λ = 1), normal (λ = 0.14) and Student (λ = -0.85) distribution, supplied with one realistic intermediate (λ = 0.1). In the first graph (Fig. 30) the number of steps taken by the animal are varied at a constant level of the scale parameter. The relation between the linear displacement and the distance walked appears to be non-linear. This result is explained on basis of the probability to return to the original position. After one step this probability is of course equal to zero. Each successive step will increase the probability of return, depending on the tortuosity of the walking pattern. However, by moving away from the original starting position the possible returning paths become more and more complex and thus less probable. In other words, the probability of leaving a circular environment decreases with enlargement of the circle. With respect to the other graphs only the linear displacement after 200 steps is given. The second graph (Fig. 31) shows an exponential increase of the linear displacement with decreasing values of the scale parameter. Seemingly small variations in the scale parameter can thus have very important consequences for the linear displacement. The third graph (Fig. 32) shows the effect of positive and negative values of the first-order auto regression coefficient. Negative correlations cause subsequent correction of sharp turns in the walking pattern by a more or less opposite turn. As can be seen from the graphs this effect substantially

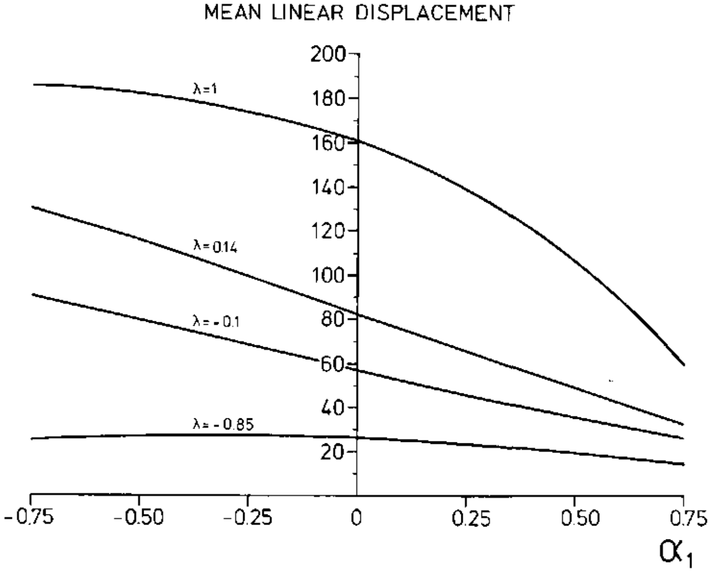


Fig. 32. Mean linear displacement, expressed in step units, in relation to the first-order auto regression coefficient α_1 at different levels of λ ($\sigma = 0.2$).

promotes the linear displacement. Positive correlations, however, intensify the turnings instead of correcting them, thus causing a decrease of the linear displacement. From these simulations it can be concluded, that within the range of measured parameter values ($-0.4 < \lambda < 0.14$; $0.1 < \sigma < 0.6$; $-0.2 < \alpha < 0.2$) the value of the scale parameter is most decisive for the linear displacement, subsequently followed by the shape parameter, while the autoregression coefficients are of minor importance.

The above method to simulate the walking behaviour of an individual animal can be extended for the case of two or more animals encountering each other. Then the animals are represented by circles and each time step is considered to be equal to the quotient of the step size and the walking velocity of the fastest animal. For each time step the positions of the circles are traced and new encounters registered if the distance between the centres of the circles is smaller than half the sum of their diameters. Such a model is listed in Appendix D for the simple case of immobile prey and equidistant distributions of the prey items. This model is used to examine the effect ot a tortuous path on the rate of encounter. Imagine an area so large that even a straight path of the predator starting at the centre does not result in a confrontation with the edge. The prey eggs are spread equidistantly and every egg crossed by the walking path of the predator is removed. Because of the large area the number of egg removals will hardly affect the value of the overall prey density. A tortuous path by the predator may give rise, however, to a frequent recrossing of a sub-area previously freed of prey, so that a prediction of the rate of encounter with the aid of Skellam's formula results in an overestimation due to its dependency on the overall prey density. On a webbed substrate predatory mites exhibit a tortuous walk, independent of the presence of prey (Subsection 3.4.1). Therefore a simulation experiment was done at a prey density of 4 eggs/cm^2 over a 1000 step walking track. The simulated mean rate of encounter after 100 replicates appeared to be equal to 81% of the Skellam's estimate. Of course, apart of the eggs and the moulting stages, the mobility of the other prey stages lower the probability on local depressions in their density. Simulations for the case of mobile larvae resulted in an estimate equal to 94% of the Skellam's estimate, so that the effect of a tortuous walk on the rate of encounter in a prey colony may be considered to be very small.

3.2.5 Walking activity

The walking activity of the predator refers to the fraction of the observation time the animal spends walking. The walking and resting periods were measured partly with the aid of the video-equipment described in Subsection 3.2.2, and partly with the aid of a binocular microscope. During the continuous observations the start and end of the walking periods were recorded on a time scale. The activity is not computed as the quotient of the total walking period and the observation time since once a mite starts walking, walking during the next time unit is very probable. Therefore to reduce these correlations, the activity is conceived as a Bernouilli variable (0 or 1) the value of which is determined at random moments during the observations within the desired limits of the relative food content of the gut. The number of determinations of the Bernouilli variable needed to attain a specified accuracy at the 5% level, were calculated with the binomial sampling formula ($\alpha = 0.05$; $d = 0.04 \times \sqrt{\min(p,q)}$; $\Pr(|p-P| \geqslant d) = \alpha$). The results are presented in Table 45.

The existence of interspecific differences in the level of activity become clear by comparison of the activity levels under webbed and unwebbed circumstances. The activity of *Phytoseiulus persimilis* decreases due to the factor web, almost irrespective of the presence of prey. In contrast, the activity of *Metaseiulus occidentalis* seems to be unaffected by the factor web and the same applies to *Amblyseius bibens*, but this species is significantly less active for abundant prey supply in the webbing (Blommers, 1977). According to the observations of the walking behaviour of *Amblyseius potentillae* it preferred the thickest parts of the ribs or similar places on the stems as a resting place. Even when they were present in a webbed area, this type of preference was observed. Its activity in the web seems to be rather low, but this is caused by the fact that only walking activities leading to displacement were scored. It was frequently observed that although this spe-

Table 45. The activity levels of *Tetranychus urticae* and females of four phytoseiid species in relation to the substrate and the time period of food deprivation. Own observations made at T = 20°C and RH = 60-80%.

Predator species	Time period of food deprivation (hours)	Activity (%) substrate		
		leaf with webbing	leaf without webbing	artificial substrates
Phytoseiulus persimilis	0 (+ prey)	8	68	75[a]
	24	9	-	30[b]
	48	16	-	-
	120	12	-	-
Amblyseius potentillae	0 (+ prey)	19	14	-
	24	17	10	-
	48	-	16	-
Metaseiulus occidentalis	0 (+ prey)	36	39[c], 52[d]	-
	48	43	-	-
	120	41	-	-
Amblyseius bibens	0 (+ prey)	46[e]	82[e]	-
	6	-	66[e]	-
	12	82	-	-
	30	97	-	-
	56	94	-	-
	120	48	-	-
	144	-	29[e]	-
	168	34	-	-
Tetranychus urticae females		4	-	72[b]
males		5	-	65-80[b]
juveniles		4	-	-

a. Takafuji & Chant (1977); T = 25°C and RH = 75-90%.

b. Mori & Chant (1966); T = 23°C and RH = 76%.

c. Kuchlein (to be published); T = 27°C and RH = 70%.

d. Fransz (1974); T = 27°C and RH = 70%.

e. Blommers (1977); T = 28°C and RH = 70%.

cies moved actively in the webbing, no effective displacement was made. On rare occasions the predator even became stuck in the webbing with its dorsum, presumably due to a lack of long dorsal setae in the centre of its dorsal plate. Under circumstances of abundant food the spider mites are much less active in the webbing than any predator species studied. This is probably due to their predominant feeding activities. When the food source became exhausted, the activity of all stages increased, leading to a steep increase of the webbing density as measured in Subsection 2.1.6.

The walking activity of the predators was unaffected after starvation periods of more than one day. However *Amblyseius bibens* showed a definite increase in activity after starvation periods of 0.5 days or more. Severe starvation induced a lower level of activity in this predator. Hungry females of all phytoseiid species were very sensitive to contact. When a female spider mite was used to bump against the back of the predators a drastic increase of the activity occurred during the subsequent two hours. Satiated females were almost unaffected by these actions. From these observations it can be concluded that the relationship between the hunger status and the activity is indirectly expressed by way of disturbance.

As found for the walking speed (Subsection 2.2.2), the effect of the temperature on the walking activity of the predators is of little or no importance, especially when the predators are studied in the webbed area of a prey colony (Table 46). Spider mites, however, are probably activated by increasing temperatures. This can be derived from the fact that the rate of web production (Subsection 2.1.6) is increased by increasing temperature, in contrast to the walking speed, which is only little affected in the range of 15-30°C (Penman & Chapman, 1980; own observation).

Mori & Chant (1966) studied the effect of humidity on the activity of females of *Phytoseiulus persimilis* and of *Tetranychus urticae*. The activity of both prey and predator was reduced by increasing humidity levels. However, although the qualitative effects of humidity were clearly demonstrated, the extrapolation of their results to the plant substrate is not allowed due to the use of an artificial substrate. Moreover the reactions of predator and prey may be different in the webbing of a prey colony.

Apart from its effect on the mean activity, the substrate also exerts an influence on the activity rhythm. In the webbed area the resting periods

Table 46. The activity (%) of female phytoseiids residing in a prey colony, in relation to the temperature level.

Predator species	15°C	20°C	29°C
Metaseiulus occidentalis	38	36	41
Phytoseiulus persimilis	10	8	12

are frequently alternated with walking periods, while on an unwebbed substrate these activities were much less fragmented; in the latter case walking periods and resting periods were longer than those for webbed substrates. This fact and the findings discussed in Subsection 3.2.3 justify a modelling approach based on random inter-arrival times of the predator between its encounters with prey items.

IV

It is of importance to stress that the factors discussed in this subsection do not determine the activity in a fixed way. For example, the level of starvation does not determine the activity level, but rather determines the level of receptivity to stimuli. Also, the substrate does not determine the level of activity nor the walking speed; hungry phytoseiid predators, when disturbed artificially, can walk very fast in the webbing structure. Disturbance by artificial means or by bumping against another mite are not the only stimuli evoking bursts of walking activity. For example, when a predatory female leaves a prey colony on her own accord (Section 3.4) and thus leaves the webbing and enters the unwebbed part of the leaf, the walking activity and the walking speed is high during the first hour and tends to stabilize towards the activity levels given in Table 45.

3.2.6 Coincidence in the webbed space

The three-dimensional structure of the webbing may cause the predator and its prey to pass above and below each other. Assuming the occurrence of the mites to be equally probable at each position in the webbing, the formula of Skellam can be easily extended to the three-dimensional case by taking the mites as spherical units and by measuring the depth of the webbing. However, a vertical section through the webbing will certainly show that the spider mites are clustered near to the leaf surface due to their predominant feeding activities. Moreover, the eggs of the spider mites are for the major part located in the lower layer of the webbing near to the leaf surface. Due to this heterogeneity an extension of Skellam's formula toward the three-dimensional case would be much too complicated, yet leaving the peculiarities in the walking behaviour of both predator and prey unconsidered. This problem can be solved more easily by multiplying the two-dimensional formula of Skellam with the fraction of real contacts between predator and prey out of all coinciding perpendicular projections on the leaf surface. The measurement of this fraction was done by observation with a binocular microscope maintained continuously in a perpendicular position above a female predator. The number of observations needed to attain a specified accuracy at the 5% level was computed with the aid of the binomial sampling formula ($\alpha = 0.05$; $d = 0.08 \times \sqrt{\min(p,q)}$; $\Pr(|p-P| \geqslant d) = \alpha$). In this way a rough estimate was obtained of the reduction of the rate of encounter due to webbing for three different phases in colony growth:

- *Phase 1* The webbing intensity brought about by female spider mites increases rapidly in the initial colonization period, but it levels off after less than a day as lateral expansion of the web becomes predominant.
- *Phase 2* After hatching of the eggs, the juveniles contribute to the production of web.
- *Phase 3* When the new born juveniles have matured, the food demands increase exponentially, so that ultimately the food source will become exhausted, causing an increase of the walking activity of all stages and, thus, an increase in the webbing intensity.

The measurements of the coincidence in these three phases are presented in Table 47. These results show that the rate of encounter is being reduced by a factor of 45-55% as a consequence of the heterogeneity of the webbing, and, that this result is, surprisingly, independent of the predator species and the prey stage involved. A more expected result was the decrease of the coincidence at the increased webbing intensity on the highly infested rose leaf. During a part of these experiments the activity status of predator and prey was taken into account (walk-walk, walk-rest, rest-walk). The re-

Table 47. Coincidence in the webbed space between female phytoseiids and different stages of their prey at three phases of colony growth. n = 350-600; prey density = 20-60 mites/cm^2; adaptation period = 12 hours; T = 20°C.

Predator species	Prey stage	Coincidence (%)		
		colony growth phase 1	colony growth phase 2	colony growth phase 3
Phytoseiulus persimilis	eggs	47.3	43.4	33.0
	juveniles	-	48.3	28.2
	females	56.2	49.0	-
Amblyseius potentillae	eggs	50.1	-	-
	juveniles	-	-	-
	females	43.2	-	-
Amblyseius bibens	eggs	47.8	-	-
	juveniles	-	46.3	-
	females	55.0	-	-
Metaseiulus occidentalis	eggs	49.1	52.2	-
	juveniles	-	46.1	24.3
	females	43.8	55.8	-

Table 48. Coincidence in the webbed space between female phytoseiids and mobile stages of their prey at three different combinations of the activity of the predator and that of the prey. Prey density = 20-40 mites/cm^2; adaptation period = 12 hours; *T* = 20°C.

Predator species	Prey stage	Coincidence (%) for activity combinations (predator-prey)		
		walk-walk[a]	walk-rest[b]	rest-walk[c]
Phytoseiulus persimilis	larvae	45.5	48.0	52.5
	females	47.5	45.0	49.4
Metaseiulus occidentalis	males	47.2	51.1	44.0
	females	50.2	49.5	48.4

a. Number of replicates per ratio = 100-150.
b. Number of replicates per ratio = 200-400.
c. Number of replicates per ratio = 150-300.

sults, presented in Table 48, do not show effects of quantitative importance. A similar conclusion was drawn from measurements of the coincidence using hungry predators (Table 49). It may therefore be stated, that - except for exhaustion of the food source of the spider mites - webbing acts as a constant 'labyrinth' in the predator-prey interaction at the colony level.

It may be worthwhile to point out the difference between the present definition of the coincidence in space and that of Fransz (1974). Fransz measured the same catalogue of behavioural components of *Metaseiulus occidentalis* on circular leaf discs of the Lima bean. In addition he recognized the problem of spatial heterogeneity in computing the rate of encounter between predator and prey on these discs. The spatial heterogeneity is caused here by the ribs and the edge of the leaf disc. Since predators prefer to walk near to these structures in absence of webbing, a smaller leaf area is scanned by the predator. Moreover, according to the experimental design of the functional response (Kuchlein, to be published; Fransz, 1974), the eggs were placed outside the ribbed area and at some distance of the leaf edge. For these reasons the edge oriented walk causes a spatial heterogeneity resulting in a reduction of the rate of encounter between predator and prey. By conceiving the problem in this way, the coincidence on the leaf discs can be determined directly as was done by the author, instead of indirectly as was done by Fransz (1974). This was accomplished by measuring the time spent walking on the ribs and near to the edges of the leaf disc, being apparently wasted time with respect to the time available for searching the

Table 49. Coincidence in the webbed space between hungry female phytoseiids and eggs of *Tetranychus urticae*. n = 150-250; prey density = 20-60 mites/cm^2; adaptation period = 0.1 hour; time of food deprivation = 2 days; observation period = 1-2 hours per predator; T = 20°C.

Predator species	Coincidence (%)
Phytoseiulus persimilis	46.6
Metaseiulus occidentalis	44.0

prey eggs. In this way it was found that 58% of the searching time (133 minutes) is being spent inefficiently. This result can be compared with Fransz's indirect method, using Kuchlein's behavioural observations on the leaf discs. He measured a walking speed of 0.47 mm/s and a walking activity of 39% in presence of prey eggs. He also measured the number of encounters during 6-hour time periods at several densities of the prey eggs on the leaf discs and found a linear relation between the number of encounters and the number of prey eggs on the 5 cm^2 leaf discs, the tangent being equal to 2.236. If the spatial heterogeneity were to be discarded, the tangent computed according to the Skellam formula on the basis of Kuchlein's behavioural observations would be equal to 5.54 (encounters per 5 cm^2 per 6 hour per egg). Dividing both the directly measured tangent by the estimated tangent, an estimate of the coincidence is obtained, which amounts to 40.2%. The rate of encounter is thus reduced by 60%, which approximates the original direct estimate closely.

3.2.7 Success ratio

After detection of a prey with its tarsal sensillae (trichobothria) of the front legs the predator may move close to its captive and subsequently its maxillary mouth parts are pushed through the integument of the prey, meanwhile inspecting the prey with its pedipalps. When this series of handlings was noticed during the behavioural observations, a successful attack II was scored, while tarsal contact led to the registration of an encounter. The fraction of successful attacks out of the total number of encounters is further referred to as the success ratio. This definition fits precisely to that of the coincidence in the webbed space, which reduces the Skellam's estimate of the rate of encounter between circular items into an estimate of the rate of tarsal contact. However on an unwebbed leaf, large and fast-walking predators inspect the area covered less intensively with their tipping front legs, which may laed to a failure to detect a small prey stage located in their *walking* path. *In that case another factor should be defined*, one that expresses the tipping intensity within the area covered by the predator's circumference. Another complication arises when the prey encounters a resting predator at the back. In the webbing, this type of prey-predator contact generally results in stimulation of the locomotory activity, but on an unwebbed substrate this sometimes caused a quick turn by a hungry predator and a subsequent attack on the prey. This apparent enlargement of the width of perception by the hungry females can be accounted for by multiplying the rate of encounter between active prey and the resting predator with *a factor, ranging from* 0.5 (no turn) to 1. (turn).

At the start of the continuous observations of the predatory behaviour, female predators were used that had been deprived of food for different periods since satiation. By transferring the predators from the Munger cages to the experimental arena with a brush severe disturbance would have been brought about very frequently. To prevent this artefact the predatory females were transferred on a leaflet, which was placed previously in the hunger cage as a refuge for the predators. In this way the predators were allowed to enter the experimental arena on their own accord.

The experimental arena consisted of a prey colony founded after a preceding infection of female spider mites on a rose leaf of an intact plant in the greenhouse. These leaves were cut off and placed upside down on wet cotton wool in a petri dish. In another series of experiments unwebbed leaves were used still connected to a part of their shoot. The shoots were put in a test-tube filled with wet cotton wool and closed by plasticine. This leaf system formed an easily turnable unit. The prey items were offered one by one to the predator, except for the prey eggs, which were deposited by female spider mites and subsequently freed of webbing and females using a brush.

During the observations the behavioural elements were scored in a time scale. These time series of observations were analyzed afterwards by computing the food content of the phytoseiid gut in a parallel time series on basis of the observed ingestion history of the individual phytoseiid females and the physiological variables measured in Section 3.1. By dividing the gut content in 20 classes of food contents the encounters between predator and prey and the eventual successful attacks among these encounters were ordered in relation to the level of the food content of the phytoseiid gut. The number of encounters needed to determine the class specific success ratio with a predefined accuracy at the 5% level was computed using the binomial sampling formula ($\alpha = 0.05$; $d = 0.1 \times \sqrt{\min(p,q)}$; $\Pr(|p-P| \geq d) = \alpha$). The number of observations per food content class were regulated to achieve the desired accuracy by manipulating the deprivation history of the starting predator and the subsequent observation time. Moreover, the 'normal' prey densities in the prey colonies happen to be quite high, e.g. the egg density ranged from 20-60 eggs per cm^2 webbed leaf area. Therefore many observations can be obtained in a reasonably short time span. Most of the observations were made at T = 20°C with colonies containing only prey eggs or only larvae and numphs or only females or only males. Some observations were done at T = 15°C and T = 29°C in colonies containing only eggs.

The results are presented in Table 50A with respect to the webbed substrate and in Table 50B with respect to the unwebbed substrate. Smoothed curves are drawn in Fig. 33 to accentuate the main characteristics. These reveal conspicuous interspecific differences among the phytoseiid species studied, when comparing the success ratios on webbed and webless leaves. The factor webbing induces a lower level of success for the case of *Amblyseius potentillae*, favours *Phytoseiulus persimilis* and hardly affects *Amblyseius bibens* and *Metaseiulus occidentalis*. II With respect to the prey-stage preference, the success ratio curves resemble each other in a qualitative sense. Because the ability of the prey to escape from an attack of the predator increases with its mobility and its strength, eggs are easier to capture than larvae, etc.; female spider mites are the most difficult stage to capture. In a quantitative respect, the prey-stage related success ratio-curves differ among the phytoseiid species studied. For each predator species on its most favourable substrate, the interspecific differences in success ratio levels suggest a relation between the body size of the predator and its predatory success. However, if the food content of the gut is expressed in weight units instead of fractions of the maximum level of gut filling, the relation of the success ratio with the satiation deficit of the gut does reveal the same but less conspicuous interspecific differences.

Some notes on the predatory behaviour underlying the measured success ratios should be made. The adverse effects of webbing on the success of *Amblyseius potentillae* may not be surprising due to the foregoing notes on the restricted mobility of this species in the webbing (Subsection 3.2.2). The effect of webbing on the success of *Phytoseiulus persimilis*, however, needs further explanation. On an unwebbed substrate this predator species walks fast and spends more time in walking. When a female predator of this species bumps into a female spider mite, it turns back and runs away with an increased walking speed, which indicates disturbance. Mori & Chant (1966) reported the very same effect. They found only 5 successful attacks among 480 contacts between *Phytoseiulus* females and *Tetranychus* females. At the side of the leaf facing downward, where the walking speed is lower but where walking activity is still high compared to that in webbing, these effects were observed to the same extent. Apparently the webbed environment, where both predator and prey walk slowly, offers a more favourable substrate for predatory activity of this species, disturbance being a rare phenomenon IV (Subsection 3.2.9). With respect to the success ratio against eggs disturbance was never observed, so that other factors operate causing the

Table 50A. The success ratios (%) of young females of four phytoseiid species[a] in relation to the developmental stage of the prey[b] and the gut filling of the predator for webbed leaf substrates. T = 20°C; RH = 70%. Each value based on 200-400 encounters.

Relative food content of the gut	Egg				Larva				Protonymph				Deutonymph ♀				Male				Female			
	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP
0- 5	55.8	89.0	96.6	93.3	-	-	44.0	-	-	-	-	-	-	-	-	-	-	-	-	-	5.7	-	14.1	79.6
5- 10	93.6	96.8	5.8	98.3	88.3	84.0	41.4	84.0	75.0	68.4	-	89.7	65.1	55.0	-	73.0	85.2	69.7	-	69.0	11.8	12.9	16.4	83.0
10- 20	85.4	91.7	4.0	89.8	73.8	76.8	44.9	88.2	59.4	60.0	-	85.7	6.2	7.8	-	66.4	4.9	16.1	51.4	72.5	1.2	2.3	2.5	83.7
20- 30	27.3	90.0	7.1	90.1	23.7	-	31.4	83.0	16.2	-	-	86.7	5.6	-	-	57.0	6.4	5.9	-	66.5	0.7	1.2	1.7	75.2
30- 40	21.7	26.5	2.8	88.4	16.6	-	34.5	84.6	15.4	-	-	83.3	1.2	-	-	63.2	1.5	-	-	64.0	0.5	0.7	1.6	71.2
40- 50	15.2	22.8	3.4	85.0	18.8	-	29.0	85.5	12.1	-	-	85.2	0.8	-	-	55.8	3.1	-	-	61.0	0.6	0.8	1.0	64.0
50- 60	10.3	24.1	5.0	85.0	5.4	-	23.4	84.1	3.1	-	-	82.9	1.1	-	-	60.3	1.1	-	43.1	72.1	0.3	0.7	1.0	51.9
60- 70	8.3	20.0	5.0	81.3	3.3	-	24.5	77.9	2.2	-	-	74.6	0.6	-	-	41.2	1.2	-	-	54.2	0.3	0.6	0.4	34.7
70- 80	4.7	19.2	2.5	78.0	3.0	4.5	15.6	70.1	1.1	-	-	64.6	1.0	-	-	44.8	0.3	-	-	48.3	0.0	0.6	0.1	24.0
80- 90	2.2	6.7	4.0	48.2	1.2	2.0	8.5	42.4	1.0	2.3	12.2	33.8	1.0	0.5	2.2	22.9	0.6	1.0	14.8	29.2	0.4	0.8	0.2	18.5
90- 95	0.7	0.7	4.4	30.9	0.4	0.4	4.1	14.3	0.2	1.2	3.0	9.8	0.0	0.0	0.8	1.2	0.6	0.1	0.8	8.7	0.0	0.4	0.0	1.5
95-100	0.3	0.0	3.2	7.4	0.1	0.2	1.0	4.5	0.0	0.1	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0

a. MO = *Metaseiulus occidentalis.*
AB = *Amblyseius bibens.*
AP = *Amblyseius potentillae.*
PP = *Phytoseiulus persimilis.*

b. Age within limits of each developmental stage was not standardized.

Table 50B. The success ratios (%) of young females of four phytoseiid species[a] in relation to the developmental stage[b] of the prey and the gut filling of the predator for unwebbed leaf substrates. T = 20°C; RH = 70%. Each value based on 200-500 encounters.

Relative food content of the gut	Egg				Larva				Protonymph				Deutonymph ♀				Male				Female			
	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP
0- 5	-	-	-	-	-	-	77.4	-	-	-	-	-	-	-	90.1	-	-	-	-	-	-	-	32.5	4.0
5- 10	91.2	96.0	52.0	8.4	81.5	85.4	90.8	21.1	76.7	-	90.6	-	-	-	85.2	-	77.0	-	88.0	2.5	12.1	13.2	30.4	4.0
10- 20	85.0	85.0	-	4.4	70.0	73.3	88.3	14.5	56.7	-	85.0	-	-	-	88.1	-	6.2	-	88.0	2.0	1.5	2.0	11.5	3.3
20- 30	24.5	60.5	-	5.0	22.7	26.2	88.0	17.8	15.5	-	80.5	-	-	-	84.4	-	4.4	-	90.3	1.2	0.6	0.9	4.0	1.0
30- 40	21.9	27.2	-	3.0	17.1	19.6	86.1	4.0	13.2	-	81.0	-	-	-	74.0	-	2.1	-	81.2	1.0	0.6	0.6	5.0	1.0
40- 50	9.0	25.0	72.0	-	-	-	72.8	-	-	-	67.8	-	-	-	63.5	-	-	-	84.5	-	-	-	4.5	0.0
50- 60	8.0	19.8	-	-	-	-	74.1	-	-	-	62.5	-	-	-	69.0	-	-	-	82.6	-	-	-	3.5	0.0
60- 70	7.4	21.0	-	-	-	-	67.9	-	-	-	68.1	-	-	-	61.4	-	-	-	72.0	-	-	-	3.0	1.0
70- 80	5.1	21.1	41.2	12.6	-	-	54.1	8.1	-	-	36.1	-	-	-	28.3	-	-	-	61.1	-	-	-	2.0	1.0
80- 90	3.4	13.3	37.5	3.1	-	-	45.2	11.1	-	-	20.3	-	-	-	14.9	-	1.0	-	54.9	0.4	0.3	0.5	0.3	0.6
90- 95	0.6	1.0	3.1	1.2	-	-	30.7	2.2	-	-	11.1	-	-	-	6.5	-	0.4	-	26.1	0.0	0.0	0.2	0.3	0.6
95-100	0.6	0.6	1.0	0.8	-	-	4.0	0.4	-	-	2.2	-	-	-	1.0	-	0.0	-	6.4	0.0	0.0	0.0	0.0	0.0

a. MO = *Metaseiulus occidentalis*.
AB = *Amblyseius bibens*.
AP = *Amblyseius potentillae*.
PP = *Phytoseiulus persimilis*.

b. Age within the limits of each developmental stage was not standardized.

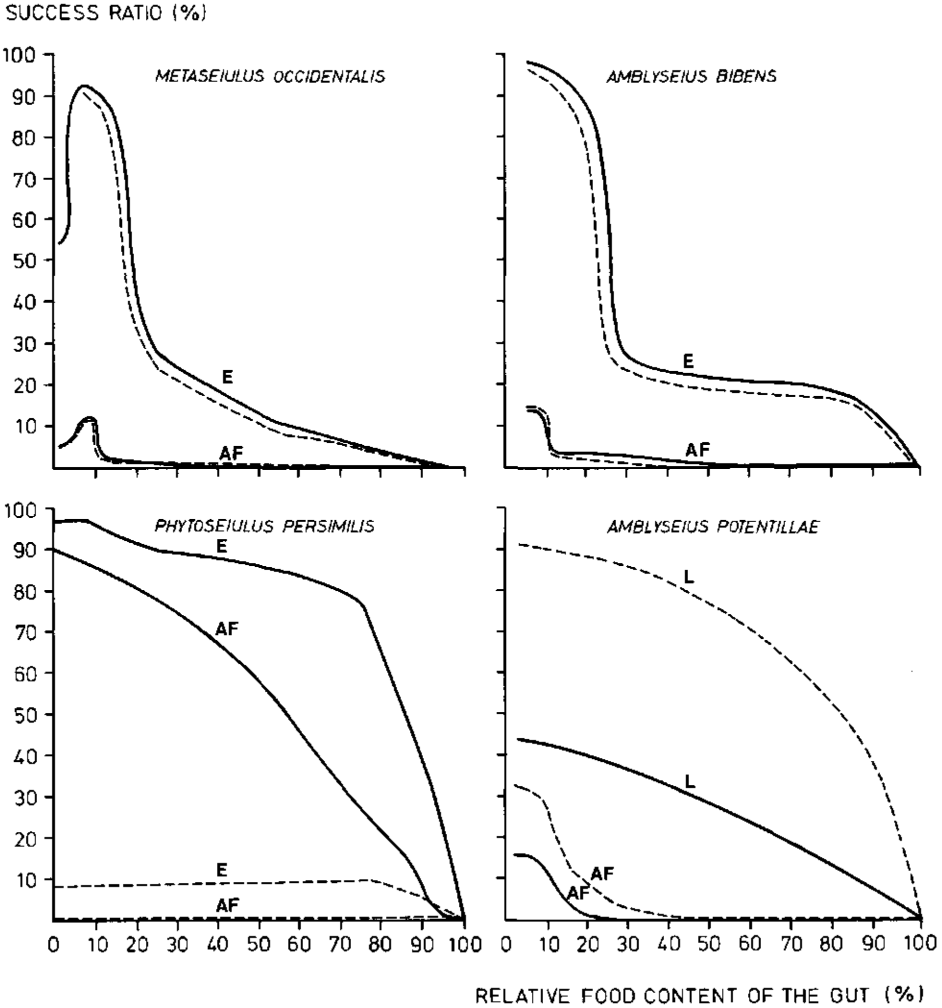


Fig. 33. Smoothed curves of the success ratio in relation to the relative food content of the gut for four phytoseiid species on small prey stages (E, eggs; L, larvae) and adult females (AF); -----, predatory behaviour on an unwebbed leaf; ———, predatory behaviour on a webbed leaf.

decreased success of *Phytoseiulus persimilis* against this stage at unwebbed substrates. Although tarsal contact occurred, the females left the eggs frequently unharmed without showing a rejective reaction, like running away. For some reason their sensitivity in detecting the presence of the prey is decreased in absence of webbing. Possibly the inspection of the substrate, being intensified in the diversely structured webbing, ensures the detection of a prey by several consecutive contacts. Anyhow it can be stated that *Phytoseiulus persimilis* is very much web oriented, being less adapted to capture a prey when dispersing from webbed area to webbed area, within which success is ensured. The disturbance described above was also observed when IV a female of *Amblyseius potentillae* bumped against an actively walking female of *Tetranychus urticae* at the side of the leaf facing upward. The behavioural reactions were very similar to *Phytoseiulus persimilis* except for the fact IV that hungry females were usually not disturbed but reacted more frequently by attack upon contact. In contrast to *Phytoseiulus persimilis*, the disturbed reactions were almost absent when the female-female contacts were observed at the side of the leaf facing downward, where walking speed is low. It may be stated that the success ratio depends on the walking speed of both predator and prey and because the walking speed varies with the type and the position of the substrate (Subsection 3.2.2), the success ratio is related to these aspects too. From this point of view it is conceivable that the small-sized phytoseiid species, like *Metaseiulus occidentalis* and *Amblyseius bibens*, are less affected with respect to their success ratio, being IV relatively sluggish and less sensitive to disturbance (Subsection 3.2.2).

Apart from the influence of the walking speed, also the locomotory activity of both predator and prey may affect the success ratio. The intensity of attack stimuli emanated by the prey may vary with the prey activity. A walking prey mite may evoke pursuit by the predator. This effect may as well IV be counteracted by a greater chance of escape. Furthermore the reaction of an active predator to active prey may differ from that of an inactive predator. For these reasons it may be worthwhile to differentiate the success ratio with respect to the state of activity of the attacker and the attacked. The elaboration of this behavioural aspect is done for the case of prey males and females (preoviposition). The results, presented in Table 51, show that IV the differences are small and far from systematic. Fransz (1974), measuring the success ratio of *Metaseiulus occidentalis* against prey males, similarly found small differences between the success ratios of active predators against active/inactive prey males (SRWW = 0.038 and SRWR = 0.034), but the resting predator seemed to react less aggressive (SRRW = 0.026). But this difference is the consequence of his definition of the success ratio, which focusses on the successfulness of mutual contacts, whether the predator was encountered frontally, laterally or posteriorly. In the present study the successfulness was measured in relation to tarsal contact. This definition is more logic from a behavioural point of view, because the predatory female first detects the prey with the tarsae of her frontlegs. A prey bumping against the back of a female predator usually evoked locomotory activation IV of the predator, rather than attack stimuli. For this reason posterior encounters with a resting predator are related to the activity level (Subsection 3.2.5) and the frequency of tarsal contact after non-tarsal contact is measured separately. The latter variable, adequately called the rate of 'turning', will be discussed below in this subsection.

To elucidate whether the temperature affects the success ratio, similar

Table 51. The success ratios (%) of females of three phytoseiid species against mobile prey items at three combinations of predator/prey activity (walk-walk, walk-rest, rest-walk). T = 20°C; webbed substrate; number of replicates per ratio = 100-300. SR = success ratio; WW = walk-walk combination; WR = walk-rest combination; RW = rest-walk combination.

Relative food content of the gut	*Metaseiulus occidentalis* vs. prey males			*Phytoseiulus persimilis* vs. preoviposition females			*Amblyseius potentillae* vs. prey males[a]		
	SRWW	SRWR	SRRW	SRWW	SRWR	SRRW	SRWW	SRWR	SRRW
0-10	82.2	86.5	86.9	81.7	80.5	82.1	87.3	88.9	88.0
10-30	5.4	4.7	5.6	75.9	77.4	76.0	90.1	87.8	88.7
30-50	1.7	2.4	2.3	66.7	68.0	68.2	81.5	83.4	82.2
50-70	1.2	0.9	1.1	44.5	41.6	42.2	78.5	75.4	77.0
70-90	0.5	0.5	0.3	21.2	18.8	22.0	55.9	57.1	56.7

a. Unwebbed substrate.

experiments were carried out at T = 15 and 29°C using prey colonies with eggs only. The results are presented in Table 52. They indicate the absence of any temperature effect. On the basis of this preliminary result it was supposed that the food content of the gut determines the probability of success, while the temperature related rate of gut emptying determines the dynamics of the success ratio. This simple hypothesis is tested in some predation and simulation experiments presented in Subsection 3.3.4.

The success-ratio curves presented in this report resemble those obtained by Fransz (1974: *Metaseiulus occidentalis* vs eggs of males of *Tetranychus urticae* at T = 25°C) and by Rabbinge (1976: *Amblyseius potentillae* and larvae of *Panonychus ulmi* at T = 18°C). The present results invariably showed a success ratio of about 90% at a low level of gut filling; this was also found by Rabbinge (1976) and corresponds with the indirectly estimated success ratios of Kuchlein (to be published). However the success ratios measured by Fransz differed largely, being always less than 50%. Croft (1972), studying the predatory behaviour of *Metaseiulus occidentalis* in relation to *Tetranychus pacificus*, measured the success ratio in a different way. He measured the percentage of successful capture by predators after two contacts with a particular prey. In the present work an encounter was scored

Table 52. Success ratios (%) of young females of two phytoseiid species in relation to the temperature. Eggs as prey; webbed leaf substrate.

Relative food content of the gut	15°C		29°C	
	MO	PP	MO	PP
0- 5	77.5	-	70.4	-
5- 10	91.4	-	82.3	-
10- 20	86.2	-	80.1	-
20- 30	30.1	-	30.8	-
30- 40	19.4	-	23.0	-
40- 50	13.8	-	14.7	-
50- 60	9.8	-	9.0	-
60- 70	-	-	-	-
70- 80	-	71.4	-	76.5
80- 90	-	47.3	-	50.1
90- 95	-	31.1	-	28.0
95-100	-	6.2	-	6.7

MO = *Metaseiulus occidentalis.*
PP = *Phytoseiulus persimilis.*

once tarsal contact was noticed, whether it was succeeded by more palpations on that particular prey item or not. The next encounter was not scored until after the predator had left the prey. Another difference with Croft's work is that he withdrew the prey after a predator had captured a particular prey stage and had assumed the feeding position. In this way the predators obtained little, if any, food, so that they could be used again after further starvation. A final difference is that encounters resulting in disturbance were excluded from the computation of the success ratio. Croft observed that direct frontal approaches of the predator to the adult female prey nearly always resulted in an avoidance response by the predators at all starvation times, and these were not counted, while they were included in the present experiments. For these reasons the results of both studies are not comparable, except for the fact that he found 90% success ratios after 1 day starvation, which corresponds with the author's results.

The effect of a less intensive inspection of the area covered by the predator was studied simultaneously during the behavioural observations. As discussed before this aspect of searching should be investigated separately at the unwebbed substrate but not at the webbed substrate, because it is implicit to the definition of the coincidence in the webbed space. The observations indicate that small prey, e.g. eggs and larvae, were only overlooked by the predatory females of the large species when walking at the side of the leaf facing upward. It was estimated that *Phytoseiulus persimilis* missed about 30% of the eggs in their walking path, while *Amblyseius potentillae* missed less than 10%. On the underside of the leaf these large predators walk more slowly and hence inspect their walking paths much more thoroughly. The other two phytoseiid species (*Metaseiulus occidentalis* and *Amblyseius bibens*) walk relatively slower and are small sized, so that any prey stage located in their walking path is detected.

An encounter of a mobile prey with the back of the predator resulted a few times in a turn of the predator towards the encountering prey so that tarsal contact occurred after non-tarsal contact. This phenomenon was very rarely observed in the webbing, probably due to the restricted mobility on this substrate. *Amblyseius potentillae*, in particular, showed a turning response on unwebbed substrates. In Table 53 the relative frequency of turns towards prey females encountering the back of *Amblyseius potentillae* (♀) are given. It is clearly demonstrated, that the width of tarsal perception is enlarged by prolonged starvation. Apart from the turning reactions the predator also reacted by forward locomotion as a consequence of the encounter. The relative frequency of this behavioural reaction is also given in Table 53. This variable, too, appears to depend on the time of food deprivation. After the prey is punctured by the predator a success is recorded; feeding starts soon after. However, it may be questioned whether feeding by the predators results in the death of the prey. Hoyt (1970) studied the mortality of different prey stages of the McDaniel spider mite after short pe-

Table 53. The relative frequency of turning of a female predator (*Amblyseius potentillae*) towards a female prey encountering the back of the predator. T = 20°C; each value is based on a minimum of 170 encounters.

Relative food content of the gut, ordered in classes	Relative frequency of turning	Relative frequency of activations
0- 20	0.64	0.29
20- 30	0.21	0.64
30- 40	0.05	0.22
80- 90	0.02	0.04
90-100	0.00	0.01

riods of feeding by females of *Metaseiulus occidentalis*. These investigations revealed that a high percentage of eggs and larvae of the prey are killed after being fed on for 5-30 seconds. Feeding periods of 30-120 seconds caused a high percentage of mortality among the nymphs and 5 minute feedings on adult female spider mites resulted in only 40% mortality, but substantially reduced oviposition by the surviving females. Van de Vrie (1973) similarly found 50% mortality among adult females of *Panonychus ulmi* after short handling periods of *Amblyseius potentillae*. He reported that this mortality was established within one day and did not increase afterwards. A comparison of the length of the above feeding periods with those measured during the present behavioural observations (Subsection 3.2.8) shows that these constitute a very small part of the total feeding period except for the rare case of an attack of a satiated female predator on a female spider mite.

Apparently the probability of a successful capture is related to the food content of the gut. However, there are two exceptions to be considered, which set limits to the applicability of this relation. First, severely starved predators can respond differently to those used in the present experiments, which are starved for no longer than 2 days at T = 20°C. In the dehydrated state, *Amblyseius potentillae* is very aggressive, as indicated by the increase of the success ratio against female spider mites for low food contents in its gut. One meal on a female spider mite would enable the gut to be filled completely, so that the subsequent probability of a successful capture is expected to be very low, according to the measurements. However, severely starved females (6 days at T = 20°C) appeared to maintain a high success ratio after their first meal, and even after their second meal the success ratio was higher than expected (Table 54). The amount of food ingested after the first meal was very low according to measurements

II

IV

IV

Table 54. The success ratio (%) of young and hungry females of *Amblyseius potentillae* against adult females of *Tetranychus urticae*. T = 20°C; observation time maximum 6 hours per individual; each value is based on a minimum of 200 encounters.

Predation history	Starvation periods	
	2 days	6 days
first success	32.5	33.8
second success	1.2	29.4
third success	-	8.4
fourth success	-	1.0

IV of the female weight, so that this predatory behaviour is induced by other motivational variables than the acquired amount of food. Presumably the persistence of aggressiveness is caused by the relaxation time of the physiological processes, leading to recovery of the metabolic imbalance. In contrast to *Amblyseius potentillae*, severe starvation of *Metaseiulus occidentalis* led to a lower success ratio than found after 2 days food deprivation. II This effect was clearly related to their loss of strength, as indicated by the decrease in walking velocity and their sluggish reactions. Both the in- IV creased and decreased aggressiveness after severe starvation are not unique for the species mentioned, but were observed more frequently in these particular cases. Apart from this lower limit to the applicability of the food concept there is also an upper limit caused by high rates of encounter with Second prey. Kuchlein (to be published) found a second rise of the rate of egg predation by *Metaseiulus occidentalis* above the density of 30 eggs per cm^2. IV Because the female predators are certainly well fed at these densities, this phenomenon can not be related to the food content of their gut but possibly to some stimulus resulting from frequent contact with prey.

These examples clearly demonstrate the limitations of food consumption as an indicator of the hunger level. Nevertheless, with respect to the range of conditions relevant in the greenhouse the use of food consumption is acceptable; for, the lower limit will be only relevant after extermination of the prey population and the upper limit at frequent prey contact is probably not met within the range of prevailing prey densities. Although the effect of frequent contact was assessed at a seemingly realistic egg density of 40 eggs per cm^2, it should be stressed that the rate of egg encounter is rather high in these experiments due to the absence of webbing. In the case of *Metaseiulus occidentalis* the difference in rate of encounter between webbed and unwebbed substrates is approximately proportional to the difference in walking velocity so that the critical egg density in a web amounts to 40 × 0.47/0.18 = approximately 100 eggs per cm^2. Such high prey densities were never measured in natural colonies grown on greenhouse roses, even with respect to all stages. These densities ranged between 20-60 prey items per cm^2 and occasionally densities up to 80 mites per cm^2 were observed. For these reasons it is allowed to apply the simple concept of food consumption for the purpose intended.

3.2.8 Handling time

The time spent handling a captured prey was also measured during the continuous observations of the predatory behaviour and subsequently it was related to the food content of the gut according to the method described in the previous subsection. The handling time consists of several activities, like palpating, piercing, feeding, 'guarding' and return feeding. Hungry predators feed almost immediately after contact with their prey, but well fed predators spend more time in initial palpating and piercing. Feeding is frequently interrupted for a short period and subsequently continued on other parts of the prey, especially when the prey is a deutonymph or an adult. A few times the predatory female seemingly left its captive, but subsequently returned towards the prey and started to feed again. At other occasions the predator was observed to sit and wait next to its captive during a handling period, cleaning its extremities in the mean time. The actual feeding period during handling amounts to 90% in the young stages of the prey and 60-70% when feeding on mature prey.

The mean handling times at different levels of gut filling are tabulated in Table 55 in relation to the developmental stage of the prey. It can be concluded that the handling time increases with developmental progression of the prey and with the period of food deprivation. The latter effect was also found by Putman (1962), Sandness & McMurtry (1972) and Fransz (1974).

Some peculiarities concerning the species studied may be noticed. *Amblyseiulus potentillae* spends little time in the handling of spider mite eggs. As discussed before, this is due to this species having some problems in piercing the egg chorion (Subsection 3.1.1). The majority of the feeding attempts fail, but successful feedings were observed too and these feeding periods were equal to those observed in the other species. Because the eggs were harmed by the piercing attempts, the time spent per egg was recorded as a handling period despite the absence of ingestion. The other species studied ingest the content of the eggs without any problem in piercing the egg chorion. *Phytoseiulus persimilis* requires less time in emptying the egg than *Metaseiulus occidentalis* and *Amblyseius bibens*. However these three species spend equal amounts of time in handling the other stages of the prey.

Table 55. The mean prey handling periods (min^{-1}) of female predators of four phytoseiid species[a] in relation to the developmental stage of the prey[b] and the relative food content of the gut of the predator. Number of replicates per computed mean = 40-110.

Relative food content of the gut	Egg				Larva				Protonymph				Deutonymph ♀				Male				Female			
	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP	MO	AB	AP	PP
0- 10	12.3	7.1	0.7	4.3	15.4	14.8	8.6	14.3	21.2	16.8	14.2	20.2	34.1	29.2	16.6	30.3	38.2	24.5	20.8	28.1	58.0	44.1	27.9	42.1
10- 20	10.8	13.2	1.3	6.2	16.1	14.0	6.3	15.6	18.3	17.2	16.3	18.7	30.8	28.0	20.4	36.2	33.4	28.1	23.4	32.7	45.6	42.0	20.6	36.8
20- 30	7.9	8.8	1.2	4.8	12.2	9.9	6.3	17.2	15.2	-	15.4	19.1	27.1	-	21.3	34.1	36.3	-	17.5	21.8	46.2	42.4	23.3	51.1
30- 40	7.7	6.2	0.6	3.6	10.4	10.4	5.4	13.1	17.9	-	13.2	15.6	29.4	-	14.6	30.1	40.1	-	26.3	22.0	39.0	36.7	18.2	44.3
40- 50	8.2	10.5	0.9	4.0	11.2	-	5.8	7.3	18.3	-	14.7	12.4	30.1	-	16.3	32.9	32.1	-	18.1	25.4	37.7	-	15.5	45.8
50- 60	7.0	9.7	1.8	4.1	10.0	-	5.3	7.8	18.6	-	10.1	14.4	23.7	-	12.8	31.1	29.3	-	18.8	23.6	29.8	-	16.0	40.5
60- 70	5.3	10.5	0.5	3.8	11.4	-	5.1	7.9	16.3	-	11.3	16.1	19.7	-	9.6	27.5	28.9	-	16.2	23.7	31.1	-	14.3	42.2
70-100	6.2	11.2	2.1	3.2	9.3	8.7	4.3	8.7	12.3	10.4	8.6	10.2	14.4	11.8	8.6	27.8	25.6	18.1	12.2	15.9	19.1	18.4	10.6	28.2

a. MO = *Metaseiulus occidentalis*.
AB = *Amblyseius bibens*.
AP = *Amblyseius potentillae*.
PP = *Phytoseiulus persimilis*.

b. Age within limits of each developmental stage was not standardized.

3.2.9 Disturbance

In the acarine predator-prey system, disturbance shows itself in several ways:

- as a decrease in the probability on a successful capture, e.g. in case of frontal encounters between a female predator and a female prey, both walking on an unwebbed, upward-facing substrate (Subsection 3.2.7)
- as an increase in walking speed, e.g. after frontal contact between active adults
- as an increase in walking activity, e.g. after contact between a resting predator and an active stage of the prey resulting in reactivation of the former (Subsection 3.2.5)
- as a decrease in the width of perception, e.g. after contact avoidance, lateral inspection by the antennae-like frontlegs (Subsection 3.2.1) decreases, resulting in a decreased width of 'antennal' perception
- as a decrease in the handling time, e.g. feeding predators being interrupted by prey bumping into the predator (Mori, 1969)
- as an increase in the success ratio of feeding predators, e.g. the prey, bumping into the predator, is immediately attacked (Haynes & Sisojevic, 1966; Sandness & McMurtry, 1972; Hoyt, 1970).

The effects of the above types of disturbance on the functional response of phytoseiid predators to prey density are considered to be very important by various authors. Mori & Chant (1966) attributed the dome shape of the functional response of *Phytoseiulus persimilis* to contact disturbance of feeding predators by the numerous female prey. Sandness & McMurtry (1972) found a second rise of the rate of predation at prey densities of 10 females per cm^2. This effect was attributed to successful attacks of the feeding predators on the prey occasionally bumping into them. Hoyt (1970) suggests, that this "two flies in one blow" principle will increase the predatory efficiency in reducing prey populations at high densities. Laing & Osborne (1974), offering prey males instead of females, did not find any decline or rise of the functional response at high prey densities.

It should be stressed that disturbance is a consequence of the vigour of the interference. Activation and disturbance are brought about by high walking speed and high walking activity. Consequently, the size of the prey and the substrate are very important. Because the above studies of the functional response were carried out on artificial substrates (paper, perspex), it may be questioned whether disturbance is important on natural substrates. Everson (1979) showed that the rate of encounter with female prey on a leaf substrate was only a fraction of that on the artificial substrates, because of their prevailing feeding activities. On a webbed leaf this reduction will be even more conspicuous due to low coincidence in the webbing, low walking speed and low walking activity. Hence it may be questioned, whether the interferences in the webbing are vigorous enough to cause disturbance and

Table 56. Walking behaviour and disturbance phenomena with respect to the mobile stages of *Tetranychus urticae* and the mature females of two phytoseiid species at high prey densities in natural colonies.

Prey stage composition of the colony	Prey density (number/ cm^2)	Predator species or prey	Walking speed (mm/s)	Walking activity (%)	Number of encounters between active prey and resting predators		Number of encounters between feeding predators and active prey		
					total	number reactivated	total	number of feedings interrupted	number of interruptions followed by attack
mobile nymphs and males (rest unspecified)	20-40	*Phytoseiulus persimilis*	0.19	9	210	17	432	5	1
		Metaseiulus occidentalis	0.20	43	376	21	394	3	0
		Tetranychus[a] *urticae*	0.09	6	-	-	-	-	-
eggs and females	20-40 10-15	*Phytoseiulus persimilis*	0.21	10	120	6	362	8	0
		Metaseiulus occidentalis	0.18	33	116	3	291	5	0
		Tetranychus[a] *urticae*	0.11	5	-	-	-	-	-

a. adult females.

whether these disturbances occur frequently at the prey densities prevailing in the greenhouse crop. This question was studied by recording the walking behaviour and the encounters in prey colonies, grown on greenhouse roses and containing a lot of mobile stages. Two types of colonies were selected:

- colonies with 20-40 nymphal and male stages per cm^2, plus a few females
- colonies with eggs and 10-15 females per cm^2.

One predatory female of *Metaseiulus occidentalis* or *Phytoseiulus persimilis* was released on each leaf and the observations started half a day later. The results are presented in Table 56. It can be concluded that for both phytoseiid species and both types of prey colonies, disturbance during feeding is a rare phenomenon and the walking speed and walking activity of both predator and prey are unaltered when compared to the data obtained in colonies containing few, or even no, mobile mites. When a female prey encountered a feeding predator, the predator mostly continued feeding and in the rare case of feeding interruption the prey captive was already sucked dry, while attack on the disturber was observed only once. Disturbance phenomena may occur upon exhaustion of the plant food source, causing the spider mites to increase their locomotory activity in search of fresh food. However this situation was not studied because it implies an infestation by spider mites that surpasses an economically acceptable damage level.

3.3 PREDATION

The predation will be modelled for the case of a predator whose gut filling determines the relative rate of successful attack (= RSE for $D_{prey} = 1$). The dynamics of the food content of the gut is simulated by integration of the rate of food intake and the rate of gut emptying over short time intervals. By assuming that each predator in a series of simultaneous predation experiments consumes uninterrupted by searching periods and at the same time acquires the same portion of food, foraging would be conceived as a deterministic process. However the random distribution of the prey and the undirected searching behaviour of the predator give rise to sequences of feeding and searching periods that are subject to stochastic variation. For this reason each predator goes through a unique time series of feeding events, so that at one moment during the predation process each predator will have a different amount of food in its gut. Therefore stochastic models of the predation process are discussed and subsequently compared with deterministic analogues to elucidate the effect of the underlying concepts.

After selection of the most adequate model from the above point of view a series of predation experiments on both webbed and unwebbed substrates are discussed and compared with appropriate simulations to validate the measured inputs and the concepts underlying that model. Subsequently it is recalled that the majority of the behavioural inputs were measured at high or zero prey density, at a standard temperature and in a standard age period, studying solitary predators only. This raises the problem of how to extrapolate those measurements to intermediate prey densities, other temperatures, age periods and predator densities? Hence a concept of the relation between reproduction and predation is proposed on the basis of experiments previously discussed in Subsections 2.2.3 and 3.1.2, which enables extrapolation in a simple way. Some validations of this concept are presented.

Finally, there is the similar problem of extrapolating measurements of 'monoculture' success ratios to 'mixed cultures' of prey stages. This is discussed on the basis of the behaviour measurements described in Section 3.2 and of the available references pertaining to prey-stage preference of phytoseiid predators.

3.3.1 Models of predation

Ensuing from the behavioural component analysis (Section 3.2), predation is determined by the food content of the phytoseiid gut, which in turn depends on food intake and gut emptying (Section 3.1). In CSMP notation, the dynamics of such a system can be simulated by the following numerical integration:

```
   FCG  = INTGRL (IFCG, RFI - RGE)
   RGE  = RRGE * FCG
```

(I)FCG = (initial) food content of the gut (µg)
RGE = rate of gut emptying ($\mu g \cdot day^{-1}$)
RRGE = relative rate of gut emptying (day^{-1})
RFI = rate of food intake ($\mu g \cdot day^{-1}$)

Because of the small time constant of the ingestion process and the short duration of the handling period needed for 90% of the ultimate food intake, ingestion may be conceived as an immediate swallow of the prey content, the size of the portion being limited by the satiation deficit of the gut (Subsection 3.1.1):

```
   RFI = AMIN1(SDG/DELT, RSE * FCP)
   SDG = GUTC - FCG
```

SDG = satiation deficit of the gut (µg)
GUTC = gut content (µg)
FCP = food content of the prey (µg)
RSE = rate of successful encounter ($prey \cdot day^{-1}$)

The rate of successful encounter can be computed from the measured behavioural components and prey density:

```
   RSE  = 1./TSC
   TSC  = FT + 1./(RRE * COIN * SR * DPREY)
```

TSC = time spent per successful capture (day)
FT = feeding time (day)
RRE = relative rate of encounter = RE/DPREY (day^{-1})

SR = success ratio (%)

COIN = coincidence in space (%)

Several of these behavioural components positively influence the rate of successful encounter at low levels of gut filling. For example, the success ratio increases if the food content of the gut decreases (Fig. 34). At a constant density of the prey, sooner or later the rate of food intake will become equal to the rate of gut emptying. Then the food content of the gut, and consequently the rate of predation, attain a constant level and the predation process enters a steady state.

However, as a consequence of predation prey density decreases unless each prey killed by the predator (or by other causes) is replaced immediately by a fresh one. Because immediate replacement is generally impracticable, the rate of predation in that case is not assessed at a steady state, due to a changing prey density. In case of fixed time delays of prey replacement the fluctuation of the prey density can be monitored during the simulation in the following way:

```
DPREY = INTGRL (IDPREY, (-RSE/AREA) + (REPL * (IDPREY-DPREY)/DELT))
REPL  = IMPULS (0., REPDEL)
```

(I)DPREY = (initial) density of the prey (prey/cm^2)

AREA = experimental leaf area (cm^2)

REPL = replacement action (0 or 1)

REPDEL = time delay of prey replacement (day)

The fluctuation in prey density can be damped by enlargement of the experimental leaf area and by shortening of the time delay of prey replacement.

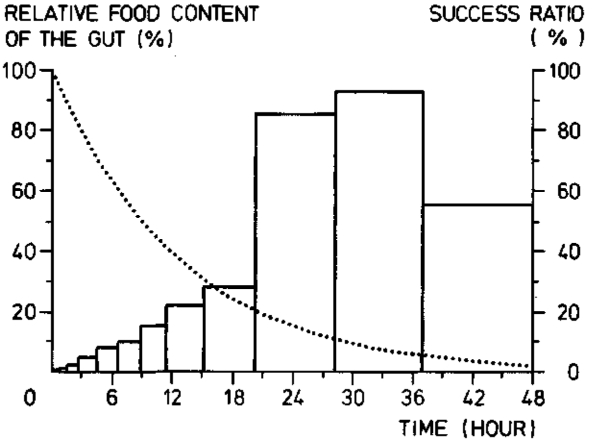


Fig. 34. Graphic display of the main counteracting processes underlying predation for young female *Metaseiulus occidentalis* and eggs of *Tetranychus urticae*. Gut emptying given by dotted line, and success ratio given by histogram.

Adequate manipulation of these measures can approximate a steady state of the predation process within the limits of practicability.

The above type of simulation (Appendix E) is called deterministic, because each moment in the predation process allows for only one possible state of the system. The predators are considered to be identical foragers, each consuming the same portion of 'crumbs' of the prey 'cake'. Moreover, consumption takes place uninterrupted by searching periods, while the size of the food portions vary in time due to the dynamics of the satiation level of the predator. It goes without saying that the actual predation process is quite different from this picture. The random distribution of the prey and the undirected searching behaviour of the predator cause the searching periods to be variable and bounded by discrete feeding periods, so that each predator has a different amount of food in its gut at one instant during the predation process. Therefore it may be worthwhile to consider stochastic models that take into account the instantaneous variation of the motivational state.

Monte Carlo simulation of the predatory behaviour may serve as a first illustration of a stochastic model. In a mite colony the searching behaviour of the predator and the spatial distribution of the prey are approximately random, so that the inter-encounter periods will be random too. In this case the inter-encounter periods, as well as the inter-attack periods (Fransz, 1974), meet the conditions of a Poisson process. The probability of no successful attacks is then equal to EXP (-RSE * TIME), so that in a sufficiently short interval (= DELT) at most one single prey can be attacked. Hence the probability of a capture in DELT is equal to:

```
PRC = 1. - EXP(-RSE * DELT)
```

PRC = probability on a capture

The capture events can be obtained from a comparison between PRC and random drawings at consecutive time intervals from a uniform distribution, ranging from 0 to 1:

```
RDRAW   = RNDGEN(U)
INCON U = 3
CATCH   = INSW(PRC - RDRAW, 0. , 1. )
```

U = starting value of the random number generator (RNDGEN)

RDRAW = random drawing from a uniform distribution ranging from 0 to 1

CATCH = indicator of a catch event (0 or 1)

When CATCH equals zero, the predator is searching; CATCH = 1 denotes a catch event. In this way sequential time intervals of searching are simulated. Interruptions for ingestion are simulated as discrete moments, so that the ingestion statement of the deterministic model can be modified as follows:

```
RFI = CATCH * AMIN1(SDG, FCP)/DELT
```

Thus food intake takes place as an immediate swallowing of the food content of the prey during a time interval in which CATCH happens to equal 1. An example of such a simulation is presented in Fig. 35, which shows the course of the food content of the gut during a foraging period.

From random draws for a series of DELTs, the feeding history of an individual predator can be simulated. To obtain an accurate estimate of the mean number of prey attacked, a large number of reruns are required, e.g. at least 100, which makes Monte Carlo simulation a computer-time consuming procedure. The program is listed in Appendix F.

The above formulation of a stochastic predation process can be extended in several ways. The capture event and simultaneous swallowing of the prey content can be replaced by an explicit feeding period and a dynamic ingestion process (e.g. Fransz, 1974; in contrast to Fransz's model, the feeding

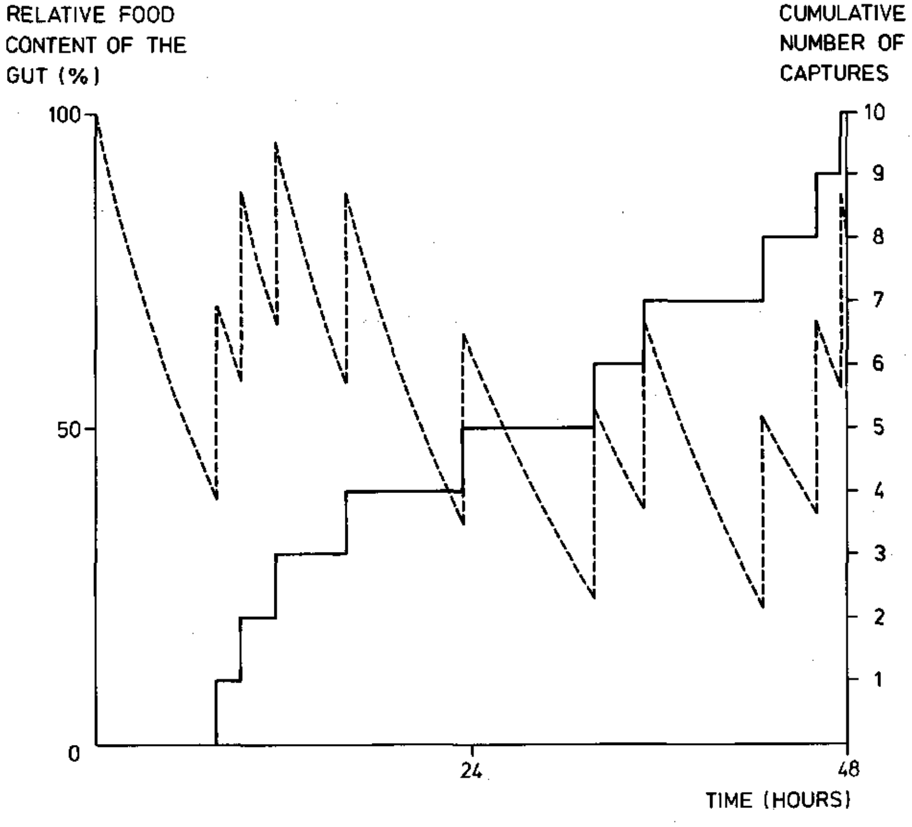


Fig. 35. Graphic representation of the predation process simulated by Monte Carlo methods (Appendix F). The dynamics of the relative food content of the gut is given by the dotted line. The cumulative number of captures during the period of predation is given by the straight line. The predator (*Metaseiulus occidentalis*) starts at full satiation and ingests prey eggs after random searching periods.

time in the model discussed above was only considered as waste time with respect to the time available for searching). Another extension can be accomplished by coupling the model of the walking behaviour of predator and prey to the above predation model, which is especially attractive in case of non-random distribution of the prey (Subsection 3.2.4). In that case the rate of encounter (RE = RRE * DPREY) is replaced by simulation of the walking behaviour of the predator (and prey) at a certain distribution of the prey. At the moment of a simulated encounter the occurrence of a successful attack can then be determined by the same type of Monte Carlo procedure but where the probability of a capture (= PRC) equals the product of the coincidence in space and the success ratio (= COIN * SR). However, because immediate swallow of the prey content is not far from reality, and the intra-colony distribution of the prey is close to being random, both extensions were considered to be irrelevant to the present problem. Besides, the minor effect of 're-crossing areas already visited by the predator' can be accounted for by simple correction if necessary (Subsection 3.2.4).

By confining the simulation problem in this way the computer-time consuming Monte Carlo simulations can be replaced by ones based on queueing theory (Saaty, 1963). Taylor (1976) and Curry & DeMichele (1977) recognized the analogy between a queue of clients, waiting to be treated by the dentist and the 'queue' of ingested prey 'waiting' in the gut to be digested, resorbed and egested by the predator. The treatment time is equal to the time needed for digestion, resorption and egestion of the mass equivalent to one prey, referred to as 'gut-emptying time'. The gut content is divided in classes, also equivalent to the mass of one prey. At full satiation (= N^{th} class) no successful captures can take place, while the rate of gut emptying equals zero in case of an empty gut (= zero class). Based on a Poisson distribution of the searching periods and an exponential distribution of the 'gut-emptying time', a set of N+1 difference equations can be derived by computing the short interval changes in the relative frequencies (= $p_n(t)$) of predators at each satiation class n ($0 \leqslant n \leqslant N$). For a small time increment DELT at most one prey can be encountered, so that $p_n(t+DELT)$ can be computed from $p_n(t)$ by summation of the following transition probabilities:

- the probability to capture and ingest one prey mass *without* simultaneous resorption of a mass equivalent to one prey, causing an increase of the food content of the gut from class n-1 to n
- the probability to capture *and* simultaneously resorb the mass equivalent to one prey, resulting in the absence of a change in the food content of the gut (= n)
- the probability of no capture *and* no resorption, resulting in a constant level in the food content of the gut (= n)
- the probability of no capture *and* one prey mass resorbed, causing a decrease of the food content of the gut from class n+1 to n.

The probability of a capture of one prey mass can be found from the following formula (CSMP notation is not used in all subsequent formulas):

$$\mathrm{PRC} = 1 - \exp(-\mathrm{RSE} * \mathrm{DELT}) = 1 - \left(1 - \mathrm{RSE} * \mathrm{DELT} + \frac{(\mathrm{RSE} * \mathrm{DELT})^2}{2!} - \ldots..\right)$$

Neglecting the terms involving DELT^2, this formula can be simplified:

$$\mathrm{PRC} = \mathrm{RSE} * \mathrm{DELT}$$

Because RSE depends on the amount of food in the gut, this formula can be rewritten by adding the suffix n, which indicates the satiation class:

$$\mathrm{PRC}_n = \mathrm{RSE}_n * \mathrm{DELT} \quad \text{and} \quad \mathrm{PRC}_N = \mathrm{RSE}_N = 0$$

The probability of the resorption of one prey mass ingested can be computed in the same way after calculation of the time needed to resorb the mass equivalent to one prey at different levels of the food content of the gut $(0 < n < N)$:

$$\begin{array}{llll} \mathrm{PRE}_n & = \mathrm{RGE1}_n * \mathrm{DELT} & \text{and} & \mathrm{PRE}_0 = 0 \\ \mathrm{RGE1}_n & = 1/\mathrm{TGE1}_n & \text{and} & \mathrm{RGE1}_0 = 0 \\ \mathrm{TGE1}_n & = \ln(n/(n-\mathrm{ONE}))/\mathrm{RRGE} & \text{for} & (1 < n < N) \\ \mathrm{ONE} & = 0.99 & & \end{array}$$

PRE = probability to empty the gut with a mass equivalent to *one* prey
TGE1 = time required to empty the gut with a mass equivalent to *one* prey

Now it is possible to give the formulas of the above four transition probabilities, which form the elements of a summation of all possible ways to arrive at satiation level n after a small time increment DELT:

- $p_{n-1}(t) * (1 - \mathrm{PRE}_n) * \mathrm{PRC}_n$
- $p_n(t) * \mathrm{PRE}_n * \mathrm{PRC}_n$
- $p_n(t) * (1 - \mathrm{PRE}_n) * (1 - \mathrm{PRC}_n)$
- $p_{n+1}(t) * \mathrm{PRE}_n * (1 - \mathrm{PRC}_n)$

Again, the terms involving DELT^2 drop out in case of small DELT, so that the distribution of the predators over the satiation classes can be simulated by recursive use of the following set of difference equations, starting from any initial distribution of $p_n(t=0)$:

$$\begin{aligned} p_n(t+\mathrm{DELT}) = {} & p_n(t) * (1 - (\mathrm{RSE}_n + \mathrm{RGE1}_n) * \mathrm{DELT}) + \ldots \\ & p_{n+1}(t) * \mathrm{RGE1}_{n+1} * \mathrm{DELT} + p_{n-1}(t) * \mathrm{RSE}_{n-1} * \mathrm{DELT} \end{aligned}$$

The expected number of prey killed per time interval (= PRED) is equal to the amount of food consumed in DELT, which can be computed from the difference between the successive distributions of the satiation levels, *plus* the amount of food resorbed from the gut during time interval DELT:

$$\mathrm{PRED} = \sum_{n=0}^{N} (p_n(t+\mathrm{DELT}) - p_n(t)) + \sum_{n=0}^{N} p_n(t+\mathrm{DELT}) * \mathrm{RGE1}_n * \mathrm{DELT}$$

The cumulative number of prey killed (= CUMPRD) is then found by adding the instantaneous values of PRED.

When prey density is kept constant by immediate replacement of the prey killed by the predator, the rate of food intake will become equal to the rate of gut emptying sooner or later, so that the predation process enters into a steady state. The relative frequencies of predators at the different satiation levels can then be solved directly by equating the differential quotients to zero:

$$p_n'(t) = \frac{dp_n}{dt} = \lim_{DELT \to 0} \frac{p_n(t+DELT) - p_n(t)}{DELT} = 0$$

The equations obtained can be rearranged as follows:

$$RGE1_{n+1} * p_{n+1} - RSE_n * p_n = RGE1_n * p_n - RSE_{n-1} * p_{n-1}$$

Because $p_0'(t) = RGE1_1 * p_1 - RSE_0 * p_0 = 0$, the right hand side of the rearranged equation is equal to zero at consecutive values of n (n = 1,2,3,...). This results in the following simple equation, showing that p_n is proportional to p_{n-1}:

$$RSE_{n-1} * p_{n-1} = RGE1_n * p_n$$

After selection of an arbitrary starting value of p_0, the values of p_n (n = 1,2,3,...) can be computed consecutively with this equation. Subsequent rescaling of the p_n values such that $\sum_{n=0}^{N} p_n = 1$ produces the steady-state distribution of the predators over the satiation classes. In this special case the formula of the number of prey killed during DELT (= PRED) reduces to the term that computes the amount of food resorbed during DELT:

$$PRED = \sum_{n=0}^{N} p_n * RGE1_n * DELT$$

Thus it is possible to compute directly the rate of predation at steady-state conditions instead of by numerical integration over small time increments. Moreover, as long as prey density is kept constant in some way, the number of prey killed can also be computed over any time interval starting from any initial distribution of the satiation levels (= $p_n(t=0)$). This is done by matrix algebra, as is shown in Appendix G. However, when the prey density is changing in time, and consequently RSE too, the set of difference equations representing the queueing process can only be solved by numerical integration over small time increments (= DELT). In the foregoing discussion of the queueing approach it was assumed that the gut content could be divided into classes equivalent to the mass of one prey. However, as shown in Subsection 3.1.1, the predatory mite does ingest the prey content partially when the satiation defecit of the gut is smaller than the food content of the prey. This aspect can be included in the Queueing model by constructing satiation classes equivalent to only a fraction of the mass of one prey (e.g. 0.5 μg). Then the amount of food ingested by the predator may exceed the amount of food equivalent to one class and can be expressed in terms of class units:

ENLARG = NCLASS/GUTC

f_n = min(FCP * ENLARG, N - n)

(SDG = N - n)

ENLARG = factor accounting for the enlargement of the gut size (and prey size) due to subdivision in satiation classes (Nclass)

f_n = food intake of a successful predator at satiation level n, expressed in class units (= INTEGERS)

In this way ingestion is represented as a discrete jump over f classes, so that the term in the queueing equations that represents the ingestion of one prey item up to state n is equal to $RSE_{n-f} * p_{n-f}$ ($f \leqslant n \leqslant N-1$), instead of $RSE_{n-1} * p_{n-1}$. The maximum satiation level can thus be attained via complete *and* partial ingestion of the prey content, i.e. starting from each class in the range of N-f to N-1. In that case the ingestion term of the queueing formula is equal to $\sum_{n=N-f}^{N-1} RSE_n * p_n$. As a consequence of partial ingestion the expected number of prey killed during DELT is not equal to the amount of food consumed. It can therefore only be computed from the term in the difference equations that accounts for the successful captures:

$$PRED = \sum_{n=0}^{N} p_n(t) * RSE_n * DELT$$

The computation of the steady-state distribution, p_n, is similar to that of the complete ingestion of the prey content. Starting from an arbitrary value of p_0, the value of p_1 can be solved from $p_0' = 0$:

$$- RSE_0 * p_0 + RGE1_1 * p_1 = 0$$

For n = 1,2,3, ... N-1 the value of p_{n+1} can be solved consecutively from $\frac{dp_n}{dt} = 0$:

$$- (RSE_n + RGE1_n) * p_n + RGE1_{n+1} * p_{n+1} = 0 \qquad (0 \leqslant n \leqslant f)$$
$$- (RSE_n + RGE1_n) * p_n + RGE1_{n+1} * p_{n+1} + RSE_{n-f} * p_{n-f} = 0 \quad (f < n \leqslant N-1)$$

Subsequent rescaling of the computed p_n values such that their sum equals 1 results in the steady-state distribution of the predators over the satiation classes (= p_n). Again, when RSE or RGE1 vary during the process, numerical solution of the difference equations is the only method that can be used.

When only discrete changes in the food content of the gut are considered, whether these are due to food intake or gut emptying, it is inevitable to express these changes in terms of probabilities, so that both the searching time and the gut emptying time are subject to stochastic varaiation. Because of the random distribution of the prey within the colony and the random searching behaviour of the predator this seems to be obvious with respect to the searching times between captures. Then the catch events occur by a Poisson process and the probability of one or more captures is given by $1 - \exp(-RSE * t)$. This quantity is a cumulative distribution from which by differentiation, one obtains the exponential density function $RSE * \exp(-RSE * t)$ for the distribution of times between captures with mean $1/RSE$ and variance $1/RSE^2$. However with respect to the gut emptying time stochastic variation seems much less obvious. Each gut content class is emptied with a probability of RGE1 * DELT during a small time increment:

$$p(t + DELT) = (1 - RGE1 * DELT) * p(t)$$

Hence

$$\frac{dp(t)}{dt} = \lim_{DELT \to 0} \frac{p(t+DELT) - p(t)}{DELT} = - RGE1 * p(t)$$

This differential equation has the solution

$$p(t) = c * \exp(-RGE1 * t)$$

Since each gut content class will be emptied sooner or later it follows that

$$\int_0^\infty c * \exp(-RGE1 * t)\, dt = 1$$

Hence c = RGE1. Thus the gut emptying time is described by the negative exponential distribution with density $RGE1 * \exp(-RGE1 * t)$. The mean gut emptying time therefore equals $1/RGE1$, and the variance is $1/RGE1^2$. From this it can be seen that because RGE1 depends on the number of satiation classes distinguished (= n), the stochastic variation in gut emptying time can be reduced by dividing the gut content into more (but smaller) satiation classes. In case of an infinite number of satiation classes the process of gut emptying is completely deterministic (variance = 0). If one wants to reduce the variance, the effect of enlarging the number of satiation classes is governed by the law of diminishing returns. Simulations indicate that the introduction of stochastic variation of the gut emptying time hardly affected the end results. Even the modification of the distribution from negative exponential to constant, uniform or normal proved to be of minor importance in a series of Monte Carlo simulations. This result was also established by Curry & DeMichele (1977). Therefore it may be stated that the choice for the class size (or the number of satiation classes) mainly depends on the accuracy one is willing to sacrifice in describing the relation between RSE_n and n. Ten to twenty satiation classes proved to be sufficient with respect to the descriptive power.

The reclassing principle shown in the queueing equations was used by Fransz (1974) in a more extended form. He also distinguished satiation classes (= n) and appropriate relative frequencies of predators (= $p_n(t)$), but he additionally recorded the mean satiation level within each class. According to the queueing approach the satiation level is only expressed in discrete class units and food intake and gut emptying are accounted for by the probability of discrete jumps from one class (n-f or n+1 resp.) to the other (= n). The reclassing method applied by Fransz is more complicated. Within each satiation class the mean food content of the gut is monitored by integrating the food intake and gut emptying. When this integration results in a satiation level outside the class boundaries, both relative frequency and the mean food content of the gut are transferred to the appropriate satiation class. After all reclassings, which are needed after a time step of integration, a weighted mean of the class-specific food content of the gut and of the matching relative frequencies of predators is computed. Due to this reclassing principle, called Compound simulation by Fransz, the process of gut emptying can be simulated in a deterministic way, while searching conserves its stochastic character. However, as stated before, Monte Carlo simulations have shown that the estimated predation is almost unaffected by the stochasticity of the gut-emptying time, whether uniform, exponential or Gaussian distributions were used. Therefore for reasons of economy the reclassing principle of the queueing approach is to be preferred since it is based on one instead of two variables per class.

A realistic aspect of the Compound model (Fransz, 1974) is that the ingestion can be integrated over small time increments instead of being represented by discrete jumps in the satiation level. Fransz accomplished this by splitting each satiation class into 2 subclasses: one with predators handling a prey and one with predators searching for prey. Each subclass is again split into a fraction of predators continuing the same occupation (handling or searching) and a complementary fraction shifting from handling to searching (= abandoning the captive) or vice versa (= catching the prey). Within the handling subclasses ingestion can be monitored by numerical integration. However one may ask whether this realistic detail is necessary: the short period needed to achieve 90% of the ultimate food intake during the total handling period and the high suction force of the ingesting predator may justify a concept of 'immediate swallow'. To establish any possible effect of the underlying concepts of food acquisition, the following models are compared for the case of a young female predator (*Metaseiulus occidentalis*) hunting for eggs of the two-spotted spider mite (*Tetranychus urticae*):

- Deterministic model (Appendix E)
- Monte Carlo model (Appendix F)
- Queueing model (Appendix H)
- Compound model (Fransz, 1974; input adapted to results of this study).

Both the Monte Carlo model and the Compound model are able to make use of separate recording of the ingestion process during the handling period. The numerical integration procedures required to accomplish this are discussed by Fransz (1974). As discussed before, the deterministic model is based on the concept of continuous feeding by identical predators, and the Queueing

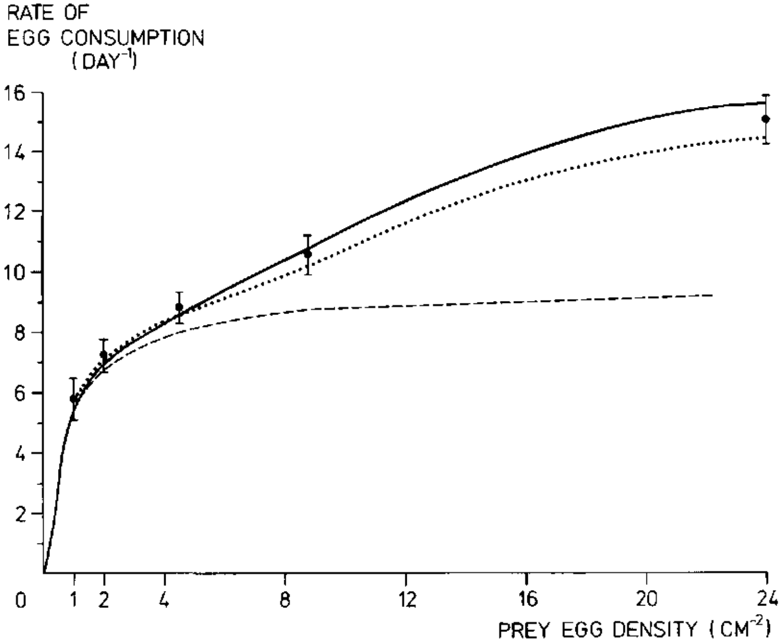


Fig. 36. Comparison between four different models of the predation process for young females of *Metaseiulus occidentalis* and eggs of *Tetranychus urticae* (T = 27°C). (Coincidence in space is not considered). ———, Compound simulation; ·····, Queueing approach; -----, Deterministic simulation; ⊥ the mean and standard deviation of 100 Monte Carlo simulations.

model is based on the concept of immediate swallowing of the prey content. The results of the simulations with these four models are given in Fig. 36. Both the Compound model and the Queueing model give predation rates that fall within the confidence limits of those obtained from the Monte Carlo simulations. It may therefore be concluded that in the present models of the acarine predator-prey system detailed representation of the ingestion process is superfluous and can be replaced by immediate swallowing of the prey. The deterministic model produces consistently lower values of the predation than all other models presented. As discussed by Fransz (1974), this difference is caused by the curvilinearity of the relation between the satiation level and several components of the searching behaviour (e.g. success ratio).

For the remainder of the simulations the Queueing model is preferred, because of its tractable mathematical properties, parsimony with respect to the number of variables and relatively economic demands on computer time. Moreover, the Queueing model can be programmed as a comprehensive subroutine, which can be coupled to the model of the predator-prey interactions on the population level (Part 2).

3.3.2 Prey density

It should be stressed that the majority of data concerning the predatory behaviour (Section 3.2) were obtained at high prey density or in complete absence of the prey. For this reason it is necessary to validate simulations of the rate of predation at intermediate prey densities. The relation between the rate of predation and prey density should be determined at standardized initial conditions (standard age, sex, feeding history, temperature, relative humidity and prey distribution), as well as at steady-state conditions during the experimental period. These conditions imply that:

- the motivational state of the predator is independent of its initial level and oscillates around a stable level
- the prey density remains constant, despite predation, by immediate replacement of the prey killed and by ruling out the possibility of reproducing or developing into a next stage.

However immediate replacement of the prey killed (or moulted) is frequently impractical, in contrast to scheduled replacement. In the latter case, prey density fluctuations depend on the time interval of prey replacement. Consequently the mean motivational state is destabilized. The fluctuation of the prey density can be damped by shortening the replacement interval and enlarging the experimental area, provided the initial prey density is kept at the same level by adequate increases in the number of prey. Due to the fluctuating prey density the rate of predation will be underestimated relative to that obtained at a constant density.

The degree of underestimation at several values of the replacement interval and of the experimental area are given in Figures 37 and 38 for a special case studied by Kuchlein (young female predator of *Metaseiulus occidentalis*, eggs of *Tetranychus urticae* as prey, unwebbed substrate, T = 25-27°C). As the density initially established declines, the underestimations become more and more severe at all schedules of prey replacement. This is a consequence of the curvilinear shape of the functional response curve: the effect of a unit change of the prey density on the rate of predation becomes more and more severe as the initial prey density declines.

The functional response, measured by Kuchlein (to be published), meets most requirements: the experimental leaf area was large (5 cm^2), the interval of prey replacement was short (0.5 hour) and the predators were standardized before use and adapted to their experimental environment for several hours. The leaf discs were put on water-soaked cotton in a petri dish, which largely prevented dispersal of the predator from the leaf disc within the experimental time alloted (6 hours). The well replicated measurements and the appropriate simulations are presented in Table 57. These correspond with each other in the range 5-30 prey eggs per cm^2. However at lower prey density the simulated predation exceeds the measured value by a factor 1.5. This deviation may be explained by a lower coincidence between predator and

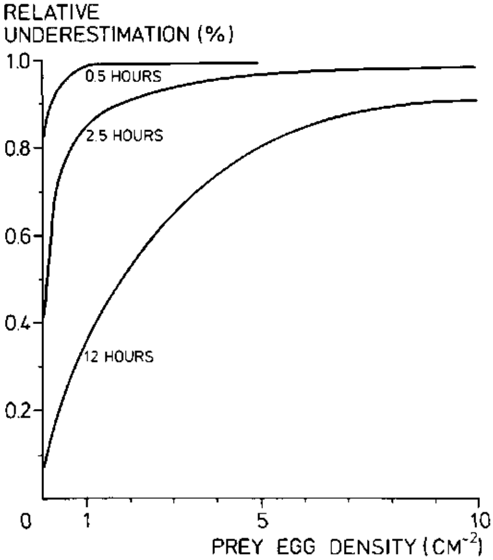


Fig. 37. Influence of the prey replacement interval on prey consumption relative to the rate of steady state predation. Experimental conditions are taken similar to those in Kuchlein (to be published) except for the experimental area (= 1 cm^2; compare with Fig. 38).

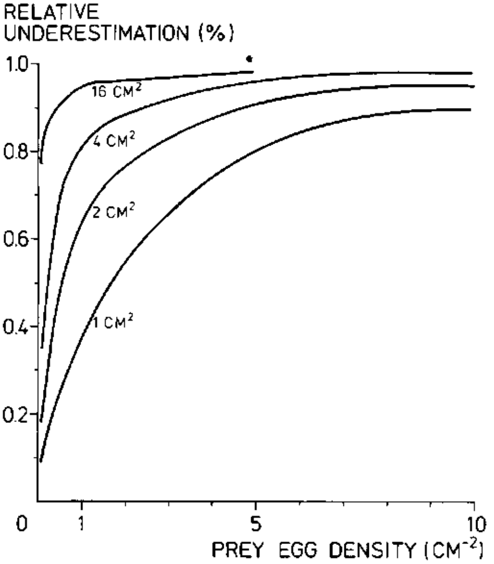


Fig. 38. Influence of the size of the experimental area at constant initial prey density on the rate of predation simulated under conditions of a 12-hour prey-replacement schedule. The underestimation of the prey consumption relative to the simulated rate of steady state predation is plotted against the initial prey-egg density. Experimental conditions are similar to those in Kuchlein (to be published).

Table 57. The functional response of Metaseiulus occidentalis to prey egg density in absence of webbing. Experimental area = 5 cm²; T = 25-27°C; unwebbed substrate of Lima bean; interval of prey replacement = 6 hours.

Number of 6-hour periods studied	Number of prey eggs per 5 cm² leaf area	Measured predation per 6 hours[a]		Simulated predation per 6 hours	Simulated predation per 6 hours using data of *Amblyseius bibens* (walking speed and walking activity)
		$\hat{\mu}$	$\hat{\sigma}$		
240	0.10	0.50	0.76	0.17	0.36
70	0.25	0.64	0.76	0.35	0.55
200	1	0.60	0.77	0.72	0.82
100	2	0.59	0.79	0.95	1.00
103	3	0.68	0.88	1.10	1.13
200	4	0.78	0.86	1.22	1.24
75	6	0.81	0.84	1.41	1.42
75	8	0.99	1.00	1.55	1.55
75	12	1.23	1.15	1.74	1.74
150	32	2.05	1.79	2.23	2.23
60	50	3.13	2.41	2.50	2.50
60	75	2.84	2.12	2.79	2.79
60	100	3.29	1.92	3.02	3.02
60	125	3.19	2.69	3.23	3.23
203	200	5.04	4.47	3.75	3.75

a. Data from Kuchlein (to be published).

prey, caused by an increased tendency towards an edge oriented walk (= dispersal). Possibly the ribs and edge of the leaf are frequented more often in this range of low prey densities than indicated by the measurements at high prey densities (Subsection 3.2.6). At very low prey densities the simulated predation becomes equal and subsequently lower than the actual measurements.

As discussed by Kuchlein (to be published), the measured predation reveals two particular phenomena at the extremes of the prey density range under investigation. Firstly the egg consumption does not decrease progressively below a food supply of 8 eggs per disc, but rather it tends to stabilize despite the decreasing prey supply. Kuchlein argues that probably the searching behaviour is stimulated by increased walking speed and activity, assuming prey is detected at tarsal contact (Subsection 3.2.3). Such a behavioural response was observed for *Amblyseius bibens*, a predator resembling *Metaseiulus occidentalis* in various respects. Hence it is interesting to include these behavioural measurement in the input for another simulation experiment. The agreement between simulated and measured predation is somewhat improved, but a full explanation of the sigmoid predation curve is still not achieved.

The second peculiarity of the functional response curve shows up at high prey-egg density. Comparison between simulation and measurement reveals a second rise of the measured predation. This difference may indicate another motivational component, which is not related to the amount of food in the gut; the piercing of the egg chorion may be stimulated by frequent contact with prey eggs. The question arises whether this level of contact frequency operates under more realistic circumstances. The prey density of 40 eggs per cm^2 is certainly relevant under field conditions. However the rate of contact at this density will be probably too high due to the absence of webbing in these experiments. The difference between simulation and measurements at high prey-egg density may be caused as well by changes in the walking pattern related to the eggs which were distributed in groups of ten eggs to easify counting; the predator may be arrested by the high egg density in the egg groups.

3.3.3 Webbing

The webbing produced by the spider mite causes the relative rate of encounter between predator and prey (= RE/DPREY) to be reduced by a factor 10 to 100. This reduction is due to the decrease of the walking speed, the walking activity and the coincidence between predator and prey in the webbing. Moreover, webbing can induce drastic changes in the success ratio (Subsection 3.2.7). Therefore distinct validation of the model and its behavioural input data is needed for the case of a substrate covered with webbing.

Including the webbing factor causes several experimental problems. First, prey replenishment turns out to be an impracticable procedure. Contact between the brush and the web threads frequently results in activation of the predator, which is sensitive to movements of the web threads. The web structure may be harmed, too, by these manipulations. Besides, positioning and settlement of the eggs by a brush may differ from the natural egg deposition of the female spider mite. For these reasons the measurement of steady-state predation is hardly possible. Simulation accounting for non-steady state conditions is the only way out then. To enable these simulations the experiments were started with fully satiated female predators and a specified initial density of prey eggs in the colony. According to Fig. 39 the underestimation of the rate of predation can be kept within certain limits by enlarging the webbed area, shortening of the experimental period and omitting the study of predation at low prey densities. Another problem is raised by the dispersal tendency of the predators. Leaf discs surrounded by a water barrier proved to be a satisfactory substrate for *Metaseiulus occidentalis*. However the leaf disc-water barrier system proved to be insufficient for the case of *Phytoseiulus persimilis*; when the prey density is low, this predator is frequently observed to disperse from the discs and to drown in the water. The best solution is therefore to use natural colonies formed on the plant and to omit the study of predation at the range of low prey densities, which

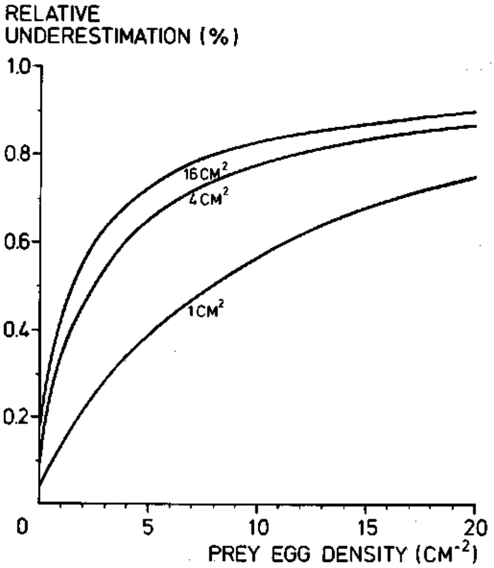


Fig. 39. Influence of the size of the webbed area at constant initial prey density on the rate of predation simulated under conditions of a 12-hour prey-replacement schedule. The underestimation of the prey consumption relative to the simulated rate of steady state predation is plotted against the initial prey-egg density. No prey-replacement; experimental period = 10 hours; T = 20°C; RH = 70%.

give rise to high dispersal tendency of the predators (see Subsection 3.4.2).

At the start of the experiments rose leaves connected to a 5-10 cm part of their shoot were cut off. Subsequently the leaf systems were placed in a water filled test tube. Young female spider mites were allowed to produce egg colonies on these leaves during 2 days at T = 25°C. Next the leaf systems were transferred to a room kept at a lower temperature (T = 20°C), to postpone hatching. After removal of the colonyfounders the webbed area was measured and the appropriate number of eggs were counted at each replicate. The size of the webbed area should exceed 4 cm^2, so that an extreme rate of predation of 20 eggs per 10 hours would cause a decrease of only 5 units of the prey density. The egg density should match some specified levels (14-15, 30-40 or 50-60), otherwise these have to be adjusted by crushing the surplus eggs with a thin needle. One young and satiated female predator was transported to the upperside of each leaf system on an excised part of its original leaf. This procedure disturbs the predator less. The predators left the excised leaf parts and entered the egg colonies within an hour. Their position in the colony was plotted for each leaf system. During the subsequent 10 hours the colonies were continuously observed one by one. The departures of the predators during this period were registered (Subsection 3.4.2), but these were not used in further calculations of the rate of predation. The results are presented in Table 58, together with simulations for matching conditions. At all prey densities tested, the simulations correspond with the measurements for both phytoseiid species studied.

Because most studies of phytoseiid predation in the past have neglected the factor webbing, it may be worthwhile to comment on their reliability

Table 58. Predation in prey colonies with spider mite eggs. Webbed area = 4-11 cm^2; no prey replacement; experimental period = 10 hours; temperature = 20°C; RH = 70%.

Predator species	Number of replicates	Range of prey egg densities	Measured predation during 10 hours		Simulated predation
			$\hat{\mu}$	$\hat{\sigma}$	
Phytoseiulus persimilis	22	40-60	9.59	3.10	8.92
	48	25-35	7.79	2.49	7.96
	20	10-15	6.71	2.12	6.50
Metaseiulus occidentalis	27	40-60	3.51	1.48	3.67
	29	25-35	3.34	1.13	3.23
	26	10-15	2.31	1.04	2.42

for the purpose of extrapolation to the population level. According to the data presented in Tables 57 and 58 the rate of predation of *Metaseiulus occidentalis* is lower on a webbed substrate (0.36 eggs per hour vs 0.55 eggs per hour). Behavioural measurements and simulations indicate that this difference is explained largely by the difference in walking speed, associated with these substrates. Besides it should be recognized that the coincidence between predator and prey eggs on the bean leaf discs used by Kuchlein (to be published) accidentally corresponds with that in the webbed space. Thus it may be stated that the artificial edge of the leaf discs contributes to the concealment of the real differences between the substrates.

Another example of the importance of the substrate is found in the case of *Phytoseiulus persimilis*, which shows drastic behavioural changes in response to webbing. The relative rate of encounter decreases by a factor 100 as a consequence of the webbing, but the success ratio is increased. Simulations based on these behavioural data show that the rate of predation on the webbed substrate exceeds that on the bare leaf disc by a factor 1.5-2. Apparently the effect on the success ratio overrules that on the relative rate of encounter. Schmidt (1976), who measured the predation of this phytoseiid on bare and webbed leaves, found a very similar difference. The data of Takafuji & Chant (1976) and Laing (1968), obtained on unwebbed substrates, are therefore likely to be underestimations of the predation rate. Laing found a predation rate of 14 eggs per day at T = 20°C, which is substantially lower than that found in this present study by direct measurement and simulation, i.e. 23 eggs per day. Takafuji & Chant found a rate of predation equal to 20-22 eggs per day at T = 25°C, which contrasts with the measurements and simulations at this temperature presented in Table 58 (i.e. about 30 eggs per day).

The female predators of *Amblyseius potentillae* showed a completely different response to the presence of webbing. The webbed areas on the leaf system were frequently avoided. The predators apparently preferred to stay near to the thickest parts of the ribs or in any cavity that can be distinguished on the stem. Much less frequently than the other phytoseiid species studied, they entered the mite colonies, where the probability of capturing prey (= success ratio) is less (Subsection 3.2.7). This probably explains the failure of *Amblyseius potentillae* to control the population growth of *Tetranychus urticae*, as found in a population experiment described in Part 2. These examples undoubtedly prove the importance of the factor webbing in the quantitative assessment of the predation capacity of phytoseiid predators.

3.3.4 Temperature

Most of the behavioural observations (Section 3.2) were carried out at T = 20°C, so that these measurements should be repeated for other temperatures. However the few additional experiments carried out at other temperatures, indicated rather unimportant effects on the searching behaviour. Temperature does exert a strong influence, however, on the food conversion physiology of the Phytoseiidae (Subsection 3.1.2). It may be assumed, therefore, that the searching behaviour is related to the food content of the gut in a way independent of temperature, while the temperature-related dynamics of the food conversion determine the rate of predation. In other words, the relation between the relative rate of gut emptying and temperature may explain the effect of the temperature on the rate of predation. This assumption is evaluated in a number of simulations and experiments concerning the rate of predation at different levels of the temperature and high density of the prey. These are presented in Tables 59, 60, 61, 62 and 63. Any measured predation rate, deviating from the simulations based on the above assumption, may indicate behavioural changes, associated with the temperature. For example the walking speed, the walking activity or the ability to capture a prey may be decreased by temperatures lower than 20°C. In theory it is possible that counteracting effects of the temperature neutralize each other, so that the resulting rate of predation does not deviate from the simulation. However it is not likely that the temperature has a positive effect on one behavioural component and a negative effect on another. It is more likely, that the effect of temperature on the searching behaviour shows one consistent tendency, if any. In that case an evaluation, as outlined above, may be a powerful tool in localizing relevant areas of further research on the searching behaviour underlying the functional response at different levels of temperature.

In Table 59 the simulated and measured egg consumption of *Metaseiulus*

Table 59. The rate of predation of two phytoseiid species (young females) at three levels of the temperature and high density of the prey in the webbed area. Prey egg density = 40-60 eggs/cm^2; webbed area = 4-11 cm^2; no prey replacement; experimental period = 10 hours; young, satiated female predators.

Predator species	Number of replicates	Temperature (°C)	Measured predation during 10 hours		Simulated predation
			$\hat{\mu}$	$\hat{\sigma}$	
Phytoseiulus persimilis	31	15	5.16	1.44	4.71
	22	20	9.59	3.10	8.92
	35	25	12.16	2.72	12.58
Metaseiulus occidentalis	27	15	2.07	1.12	2.19
	27	20	3.51	1.48	3.67
	22	25	4.57	1.41	4.92

Table 60. The rate of predation of *Metaseiulus occidentalis* at different levels of temperature and high density of the prey. Number of prey eggs per leaf disc = 100; leaf area = 5 cm²; unwebbed substrate; the prey eggs killed were replaced after one day = adaptation period of the predator; subsequent period of 1 day = experimental period.

Number of replicates	Temperature (°C)	Egg consumption per day[a]		Simulated egg consumption
		$\hat{\mu}$	$\hat{\sigma}$	
71	15	4.73	2.95	5.23
76	21	10.09	5.94	9.82
64	26	13.16	-	13.57
68	33	14.87	6.30	15.30

a. Unpublished data from Kuchlein.

Table 61. The rate of predation of *Amblyseius bibens* at different levels of the temperature and high prey density. Prey egg number = 40; leaf area = 4.5 cm²; unwebbed substrate; the prey eggs killed were replaced after one day = adaptation period of the predator; subsequent period of 1 day = experimental period; eggs of *Tetranychus neocaledonicus*.

Number of replicates	Temperature (°C)	Egg consumption per day[a]		Simulated egg consumption
		$\hat{\mu}$	$\hat{\sigma}$	
32	18	4.4	1.8	7.5
21	22	9.7	1.8	10.3
30	25	13.4	2.2	13.5
25	28	17.2	1.7	16.6
37	31	21.2	2.3	18.9

a. Data from Blommers (1976).

occidentalis and *Phytoseiulus persimilis* is given for three different levels of temperature and high prey density. These experiments were carried out on webbed leaves according to the procedure discussed (Subsection 3.3.3). There is a striking correspondence between the simulated and measured predation, which indicates the absence of relevant effects of the temperature. The same

Table 62. The rate of predation of *Amblyseius potentillae* at different levels of temperature and at different densities of the larvae of *Panonychus ulmi*. Leaf area = 3.8 cm² (or 7.6 cm²); unwebbed apple leaf of 'Golden Delicious'; interval of prey replacement = 15 minutes (T = 25°C) or 1 hour (T = 15°C); experimental period = 1 day; predators are adapted to the environmental circumstances for several hours.

Number of replicates	Temperature (°C)	Number of prey per leaf disc	Prey consumption per day[a]		Simulated prey consumption
			$\hat{\mu}$	$\hat{\sigma}$	
16	15	0.5	1.7	1.45	3.32
24		1	2.7	1.15	4.29
10		5	9.9	6.2	7.46
2	18	1	6.0	-	6.11
8		2	7.7	10.1	7.91
8		5	9.7	10.2	10.94
5		10	12.0	7.6	13.57
4		25	19.4	11.4	16.94
20	25	1	13.4	9.1	9.43
12		5	23.0	13.1	17.81
8		10	24.0	3.9	21.90

a. Data from Rabbinge (1976).

conclusion can be drawn from a similar analysis of the experiments of Kuchlein with *Metaseiulus occidentalis* over a broad range of temperatures (Table 60). On the contrary the analysis of Blommers's experiments with *Amblyseius bibens* reveal an effect of the temperature (Table 61); the simulations at low temperature result in an overestimation of predation, those at high temperature result in an underestimation of the predation. Apparently the searching behaviour of *Amblyseius bibens* is stimulated by high temperature, while it is less effective at low temperature. Another indication for such a role of the temperature can be obtained from an analysis of Rabbinge's (1976) data concerning *Amblyseius potentillae* and *Panonychus ulmi* as prey (Tables 62 and 63). Assuming that the fruit-tree red spider mite and the two-spotted spider mite are identical as prey, the functional response of *Amblyseius potentillae* to the density of the larvae and adult females of the spider mite are simulated. Comparison between the data and the simulations again shows a tendency to overestimate the predation at low

Table 63. The rate of predation of *Amblyseius potentillae* at different levels of temperature and at different densities of the adult females of *Panonychus ulmi* (eggs of *Panonychus ulmi* were not consumed). Leaf area = 3.8 cm^2 (or 7.6 cm^2); unwebbed leaf of 'Golden Delicious'; interval of prey replacement = 15 minutes (T = 25°C) or 1 hour (T = 15°C); experimental period = 1 day; predators are adapted to the environmental circumstances for several hours.

Number of replicates	Temperature (°C)	Number of prey per leaf disc	Prey consumption per day[a]		Simulated prey consumption
			$\hat{\mu}$	$\hat{\sigma}$	
16	15	0.5	0.91	1.03	0.70
24		1	1.17	0.43	1.03
11		5	1.09	1.62	2.42
20	25	1	2.55	3.12	1.89
12		5	6.99	3.60	4.47
8		10	6.38	5.18	6.55

a. Data from Rabbinge (1976).

temperature (15°C) and to underestimate at high temperature (25°C), while there is correspondence at intermediate temperature (18°C).

Indeed there are some direct measurements of the searching behaviour that indicate that it is affected by temperature, though only slightly. For example, the walking speed increases somewhat for an increase in temperature (Subsection 3.2.2). It is quite possible that the walking activity or even the ability to capture a prey are affected too. However before suggesting the need of further experimentation it should be stressed that the effect of the temperature on the walking speed, as well as that on the predatory searching behaviour, was studied on unwebbed substrates facing upward. For webbed substrates, which are the usual substrate for any predator foraging on the two-spotted spider mite, similar analyses showed that temperature had no effect on predatory searching behaviour. This result corresponds with the assessment of only minor effects of the temperature on the temperature on the walking speed in the webbed area (Subsection 3.2.2). In addition in the case of the fruit-tree red spider mite, which does not produce web aggregates, it is more careful to study the effect of temperature on the searching behaviour at the side of the leaf facing downwards, because there the walking speed of Phytoseiidae is reduced to 15-25% of values for the upperside of the leaf and the effect of temperature on the walking speed may consequently be small.

3.3.5 Age and oviposition history

So far only young females, aged 3-8 days after their final moult, have been considered in this chapter. Because the population model of the predator-prey interaction includes predation at all phases of ageing, the behavioural study of the phytoseiids should be extended accordingly. However, before doing so, the need for further experimentation is considered. It may be assumed tentatively that the ability to capture a prey successfully is constant with age in contrast to the conversion of food (digestion, resorption, synthesis and allocation). In other words, the relative rate of successful encounter (= RSE_n, if DPREY = 1, $0 \leqslant n \leqslant N$) are constant during the whole period of female adulthood, but the relative rate of gut emptying (= RRGE) is variable in this respect. In this case any change in the rate of predation during the adult period is thought to be caused by a change in the intrinsic food utilization of the predator apart from changes in the prey density. If this conception is true, it is sufficient to measure the behavioural components at one specific age period, while the age related changes in the relative rate of gut emptying can be estimated from the reproduction curves, presented or referred to in Subsection 2.2.3, with the aid of the model of mass expenditure in the phytoseiid body (Subsection 3.3.2). These assertions will now be evaluated against experimental observation.

The assumption that RSE_n is constant with age can be evaluated by comparison of the observed predation rate of females of different ages that have the same level of food conversion. This is achieved by comparing the predation of non-ovipositing females of different ages:

- unmated young females (2-4 days after final moult)
- unmated old females (about 30 days after final moult)
- 'young' postoviposition females (25-35 days after final moult)
- 'old' post-oviposition females (45-55 days after final moult).

These females are supposed to have the same level of food conversion because their weights are approximately equal and the synthesis of protoplasm only serves to replace old protoplasm ('non-growing system'). In addition to direct measurement, predation can also be simulated (Subsection 3.3.1). The relative rates of successful encounter (= RSE_n, if DPREY = 1, $0 \leqslant n \leqslant N$) are obtained from the 3-8 day females (Section 3.2) and using the model of phytoseiid mass expenditure (Subsection 3.3.1) under conditions of satiation, a value of RRGE can be fitted such that the weight loss by transpiration and respiration (= fresh weight minus food content of the gut, multiplied by the relative rate of weight loss; see Subsection 2.2.5 and Section 3.1) are compensated by resorption of food from the gut store. The simulations of the rate of predation on basis of these input data correspond with the values obtained with unmated young and old females and the 'young' post-oviposition females (Table 64). The predation of the 'old' post-oviposition

Table 64. The rate of egg consumption by non-ovipositing females of different ages. T = 20°C; webbed area = 4-11 cm^2; prey egg density = 40-60 eggs per cm^2; no prey egg replacement; experimental period = 1 day; number of replicates = 10-15.

Predator species	Measured predation (eggs per day) by unmated females of 2-4 days old		Measured predation (eggs per day) by unmated females of 30 days old		Measured predation (eggs per day) by postoviposition females of 25-35 days old		Measured predation (eggs per day) by postoviposition females of 45-55 days old		Simulated predation
	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\mu}$
Phytoseiulus persimilis	10.1	2.3	9.8	1.9	9.7	1.8	8.0	1.9	9.7
Amblyseius bibens	4.9	1.2	5.2	1.2	4.8	1.0	4.3	1.2	5.3
Metaseiulus occidentalis	4.7	1.6	4.5	1.3	4.4	1.4	3.8	0.9	5.0

females is somewhat lower than the others, which indicates a slight effect due to ageing. However this effect can also be left out in simulations of the interaction between predator and prey populations, because the fraction of the females reaching this phase of adulthood (50 days) is small, anyway. For this reason the simulations on the population level have been based on the assumption of searching ability, which is constant with age.

The second assertion of a variable relative rate of gut emptying (RRGE) with age is therefore probably true, because the reproduction has a curvilinear relation with age (Subsection 2.2.3). The relation of RRGE to age appears to have a flexible character due to the strong tendency among the Phytoseiidae to achieve the deposition of a specified number of eggs, for, as argued in Subsection 2.2.3, the rate of reproduction does not depend on age, but rather on the number of eggs already deposited. Because reproduction depends on the delivery of gut stores, reproduction can be modelled by relating the relative rate of gut emptying to the oviposition history of the predatory female (= the proportion of the potential fecundity that has been realized). In Subsection 3.1.2 it has been shown that direct measurement of the RRGE corresponds with its indirect estimation by a model of the phytoseiid mass expenditure. Therefore this model has been used for the appropriate rates of reproduction to estimate RRGE for several 'history' classes. These estimates were made for the case of ample food supply, so that as well as the rate of reproduction, the food content of the gut is known. Thus the relative rate of gut emptying can be fitted in the mass expenditure model. For sufficient description of the changes in the food conversion, the oviposition history should be divided into at least four episodes (classes) with respect to the realized part of the potential fecundity:

- less than 60% of the eggs deposited
- 60-85% of the eggs deposited
- 85-100% of the eggs deposited
- all eggs deposited (= post-oviposition period).

The appropriate values of the relative rate of gut emptying are given in Table 65. These estimates were obtained from the reproduction curves presented or referred to in Subsection 2.2.3, which were obtained at conditions of abundant food supply. The estimates were evaluated at low prey-egg densities for the case of *Metaseiulus occidentalis*, using data of its reproduction history (Kuchlein, to be published) and simulations of the egg consumption at the appropriate conditions (predation was not measured in the same experiment). Because estimates of predation at all prey-egg densities were available and the RRGE values of each history class were estimated from the reproduction curve at a high prey density (150 eggs per 5 cm^2), the rate of reproduction at lower prey-egg densities were simulated with the model of mass expenditure, and subsequently the estimated and measured reproduction curves were compared (Fig. 40). The agreement was quite satisfactory for the period 0-50 days, but when the age of the predator exceeded 50 days,

Table 65. Estimations of the slope of the relation between relative rate of gut emptying (RRGE) and temperature at four phases in the oviposition history (RRGE = SLOPE × (temp. - 11).

Predator species	SLOPE ($day^{-1} \cdot °C^{-1}$) for history class 1[a]	SLOPE ($day^{-1} \cdot °C^{-1}$) for history class 2[b]	SLOPE ($day^{-1} \cdot °C^{-1}$) for history class 3[c]	Postoviposition history class 4	Valid range of temperatures
Phytoseiulus persimilis	0.21	0.11	0.08	0.04	13-33°C
Amblyseius potentillae	0.15	0.09	0.07	0.04	13-26°C
Amblyseius bibens	0.20	0.1	0.07	0.04	13-33°C
Metaseiulus occidentalis	0.195	0.1	0.07	0.04	13-30°C

a. 0-60% of potential fecundity realised.

b. 60-85% of potential fecundity realised.

c. 85-100% of potential fecundity realised.

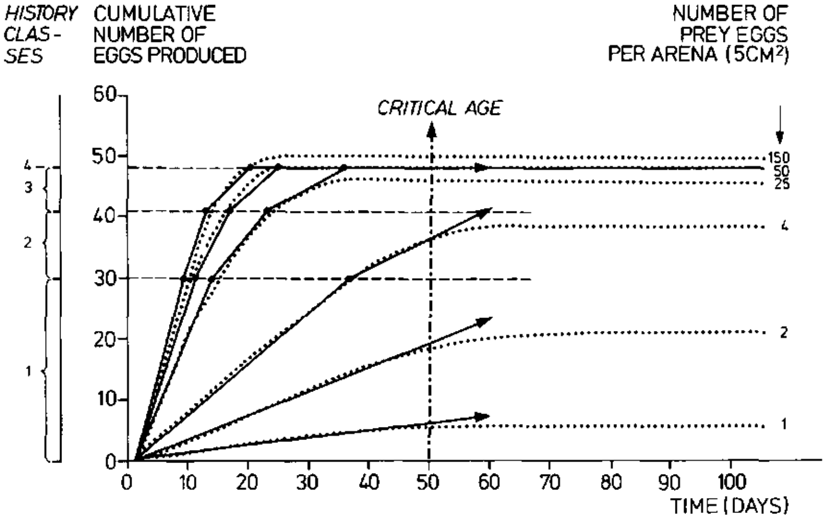


Fig. 40. Cumulative reproduction in relation to age and oviposition history of *Metaseiulus occidentalis* at different levels of prey-egg density. Measured data of Kuchlein (to be published) (·····) and simulated values (———). Unwebbed leaf disc; area = 5 cm²; daily replacement of eggs consumed; T = 25-27°C; RH = 70%.

reproduction stopped, irrespective of the oviposition history. Because relatively few females reach this period of adulthood, this aspect may be ignored in simulations of the interaction between predator and prey populations. Unfortunately, such evaluations of the estimated values of RRGE could not be carried out for the other predator species because of lack of reproduction-history data at low prey densities and for the whole life-span of phytoseiid females.

3.3.6 Predator density

When predators aggregate in colonies with a high prey density, it is likely that they will encounter each other while searching for prey. This contact may in turn lead to an increased tendency toward dispersal (Subsection 3.4.3) or, if the predators are confined to the prey colony, to a decreased prey consumption. The latter case will be considered below.

Kuchlein (1966) observed a decrease in the rate of reproduction of *Metaseiulus occidentalis* at predator densities exceeding one female per leaf disc. Fernando (1977) found a decrease of the rate of predation by females of *Phytoseiulus persimilis*. Because the ingested food is utilized to a great extent in egg production, reproduction decreases when prey consumption decreases.

A decline in the rate of prey consumption can be caused by a decrease in:

- the rate of contact with prey items (i.e. RRE)
- the receptivity to contact with prey (i.e. Success ratio)
- the rate of food conversion (i.e. RRGE).

Because the time predators spend in contact with each other is neglegible, and the walking speed and activity remain unchanged after mutual contact (own observation; Kuchlein, personal communication), the time available for prey searching remains nearly unchanged, at realistic predator densities and therefore the first possibility can be cancelled. The latter two explanations are difficult to illustrate by experiment. It may be hypothesized that the reproduction site in the acarine functions as a 'sink' with respect to the need for food and that this 'sink' is controlled by the neurophysiological state of the predator. Mutual contact between predatory females may affect that state and hence the need of food for egg production. If the prey-capture ability is not affected by previous contact, the decreased rate of prey consumption is the simple result of a decreased rate of food conversion. This is a simple mechanism because it requires only a change in the relative rate of gut emptying instead of changes in the success ratios at several levels of gut filling.

For the time being this explanation is pursued and hence the effect of interference among female predators can be modelled by estimating RRGE from the reproduction curves at different levels of predator density, measured by Kuchlein (1966) for the case of *Metaseiulus occidentalis*. This estimation is again made with the model of the mass expenditure (Subsection 3.1.2), assuming that the success ratio is unaffected by mutual interference. Even if this tentative conception turns out to be biologically invalid afterwards, it is still a very easy way of imitating the observed effects of predator density on the rate of predation. The estimated values of RRGE are given in Table 66 for different phases in the oviposition history of the predatory mites.

3.3.7 Prey stage preference

If prey stage preference is not expressed until the moment of contact with a prey stage, it can be defined quantitatively by the differences between the success ratios related to the different prey stages (Subsection 3.2.7). Preference thus defined includes the defensive measures taken by the prey, and the palability of the prey, as well as the aggressiveness and attacking measures taken by the predator. The success ratios have been measured in 'monocultures' of each prey stage (Subsection 3.2.7). These data are suitable for extrapolation to 'mixed cultures' of prey stages if the actual success ratio is not altered by experiences at 'past' contacts with prey stages, and if this ratio is determined merely by the actual amount of food in the gut, which is the result of 'past' ingestion and 'past' conver-

Table 66. Estimations of the relation between the relative rate of gut emptying, the oviposition history and the predator density for the case of *Metaseiulus occidentalis*. T = 25-27°C; RH = 70%.

Predator density (number per leaf disc of 5 cm²)	RRGE (day^{-1}) for history class 1[a]	RRGE (day^{-1}) for history class 2[b]	RRGE (day^{-1}) for history class 3[c]	RRGE (day^{-1}) for history class 4[d]
1	3.0	1.5	1.05	0.6
2	2.25	1.35	1.05	0.6
4	1.65	1.2	0.9	0.6
10	1.2	0.9	0.75	0.6

Data derived from Kuchlein (1966).

a. 0-60% of potential fecundity realised.

b. 60-85% of potential fecundity realised.

c. 85-100% of potential fecundity realised.

d. Postoviposition

sion of food.

Under this assumption the predation in mixed populations of prey stages can be simulated on the basis of behavioural input data measured in populations of one stage at a time. The Queueing model can be adapted to the case of mixed populations by extending the 'ingestion' term in the set of difference equations, which relate $p_n(t+DELT)$ to $p_n(t)$ (Subsection 3.3.1). The food level n of the gut can be arrived at by ingestion from several lower levels due to the different food contents of the prey stages (= FCP^s; s = 1,2, ... S = prey stages labeled by enumeration), which are swallowed immediately after capture. The size of the food intake depends on the food content of the prey stage and the satiation deficit of the gut (= N-n).

$$f_n^s = \min(FCP^s * ENLARG, N - n)$$

Hence the probability to reach state n via prey capture and subsequent ingestion consists of the sum of the probabilities on each - prey stage specific - ingestion (= FCP^s), which arrives at state n:

$$I_n = \sum_{s=1}^{S} RSE_{n-f}^{s} * p_{n-f} * DELT \qquad (f = FCP^s * ENLARG;\ N\text{-}n > FCP^s)$$

At full satiation it includes, furthermore, the sum of the probabilites on each possible partial ingestion, which arrives at N:

$$I_N = \sum_{s=1}^{S} \sum_{n=N-f}^{N-1} RSE_n * p_n * DELT \qquad (f = FCP^s * ENLARG;\ N\text{-}n \leqslant FCP^s)$$

The complete set of difference equations is then:

$$p_n(t+DELT)=p_n(t) * (\sum_{s=1}^{S} RSE_n^s + RGE1_n) * DELT + p_{n+1}(t) * RGE1_{n+1} * DELT + I_n$$

$$p_N(t+DELT)=p_n(t) * RGE1_N * DELT + I_N$$

The expected amount of food consumed per time interval DELT (= CONS) can be computed from the difference between the successive distributions of the satiation levels, *plus* the amount of food resorbed or egested from the gut during DELT:

$$CONS = \sum_{n=0}^{N} (p_n(t+DELT) - p_n(t)) + \sum_{n=0}^{N} p_n(t+DELT) * RGE1_n * DELT$$

The expected number of each prey stage killed during DELT can be computed from the product of the relative frequencies of predators at the different satiation levels and the appropriate prey stage specific rate of successful capture:

$$\mathrm{PRED}^s = \sum_{n=0}^{N} p_n(t) * \mathrm{RSE}_n^s * \mathrm{DELT}$$

The steady state distribution of the predators over the satiation classes (= p_n) can be computed in a way analogous to that discussed in Subsection 3.3.1. In case RGE1 and RSE are varying during the process, numerical solution of the set of difference equations is the only way out.

With the aid of this model extension it is possible to extrapolate the input data measured in 'moncultures' of the prey stages to the case of mixed populations of prey stages. This approach can be validated using experimental data of Rabbinge (1976). He offered 10 spider mites of two distinct prey stages (larva and adult female) to a young female *Amblyseius potentillae*. The prey stages were offered in different proportions (8:2, 5:5, 2:8), which were maintained by replacing the prey killed (or moulted) after in-

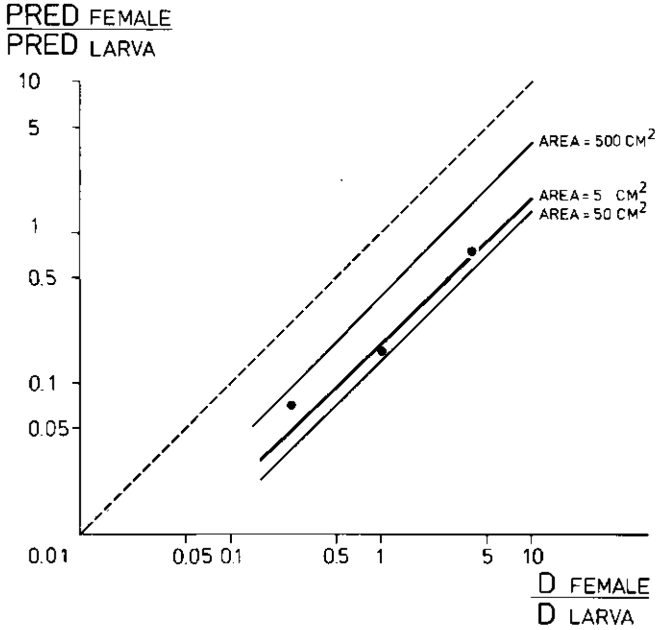


Fig. 41. Measurements (Rabbinge, 1976; Experimental area = 5 cm²; interval of prey replacement = 1 hour; T = 25°C) and simulations (this report) of prey-stage specific predation in mixed populations of two prey stages (larvae and adult female of *Panonychus ulmi*). The quotient of the prey stage specific predation rates is plotted against the quotient of the respective densities of the prey stages, both on a logarithmic scale. Measured values (●) at 3 prey stage combinations: 2 ♀ + 8 larvae; 5 ♀ + 5 larvae; 8 ♀ + 2 larvae. Simulations (———) at 3 overall prey densities: $D_{prey} = D_{female} + D_{larvae}$ = 10/AREA, where AREA equals 5, 50 or 500 cm².

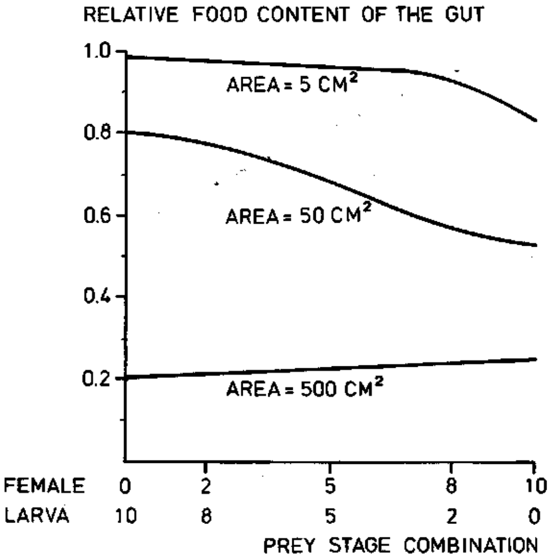


Fig. 42. Simulated mean level of the gut filling at three overall prey densities, consisting of different combinations of larvae and females. This plot fits to the simulation experiments presented in Fig. 41.

spections at short time intervals (1 hour). By assuming, that the prey stages in question resemble the two-spotted spider mite in their role as prey, these experiments can be simulated on basis of the behavioural data of this Agricultural Research Report. The results are presented in Figures 41 and 42 as a plot of the quotient of the prey stage specific predation rates against the quotient of the respective densities of these prey stages (2:8, 5:5, 8:2). The simulations agree with the experimental data if the larvae constitute half or more of the prey population. When the adult female preys form the majority, however, the predation of this particular stage seems to be favoured in comparison to its simulated predation. Presumably this effect is caused by a disturbing effect of some contacts between adult female predators and the large-sized female prey. The contact caused the predator to be less attentive in localizing the small sized larval prey.

The success ratio curves presented in Subsection 3.2.7 show that prey stage preference is strongly related to the size of the prey. Moreover these data suggest, that the preferences tend to vanish as the satiation level of the predator decreases. This effect is demonstrated in Fig. 42 with the aid of simulations at lower levels of the prey density (= enlarging the experimental area). At a prey density of 0.2 (= 10/50 cm^2) the larvae are captured more successfully than at the density of 2 (= 10/5 cm^2). A further decrease to the very low density of 0.02 (= 10/500 cm^2) tends to render the predator less fussy with respect to both prey stages. Hence it is shown that preference could be far from a stable phenomenon. For this reason the use of descriptive formulas of the functional response curve - like the Disc equation (Cock, 1977) or other equations (Rabbinge, 1976) - in analyzing preference is discouraged: fussiness of the predator is likely to depend on the food content of the gut (or the availability of the prey).

3.4 RATE OF DEPARTURE

So far the predatory behaviour has been considered isolated from any tendency to leave the prey colony. By staying in a colony, predation decreased the food supply of the predatory female and, also, its progeny. Therefore departure to other colonies is likely to occur sooner or later. Moreover, as predators aggregate in colonies with high prey density, it is increasingly likely that they will detect each other while searching for prey, which may lead to an increased tendency toward dispersal. This section deals with the quantitative assessment of the rate of departure in relation to prey supply and interference between phytoseiid females, but before discussing these measurements the walking behaviour of the predator and the size of the colonized area on residence time in a colony is investigated. Due to its apparent avoidance of the webbed area *Amblyseius potentillae* has been excluded from the measurements.

3.4.1 Walking behaviour

As discussed in Subsection 3.2.4, it is possible to simulate the walking behaviour and the linear displacement, based on analysis of measured walking tracks. This simulation technique could be used to estimate the rate of departure, assuming the edge of the colonized area exerts no influence on the walking pattern. Before turning to such simulations it should be recalled that the walking paths of Subsection 3.2.4 were measured in absence of prey or other predators. Therefore it is necessary to ascertain whether the walking pattern is modified by their presence. The observations were made with the video equipment, described in Subsection 3.2.4, to copy the walking paths. The paths were registered for 1 or 4 predatory females walking inside a fresh prey colony (eggs and females). The parameters of the experimentally defined frequency distributions of angular deviations were used to estimate the linear displacement after 200 steps. These estimates, together with the walking speed and activity, are given in Table 67. They can be compared with the results of Subsections 3.2.2 and 3.2.5. This clearly demonstrates that the walking pattern is not affected by prey or predator density, nor the walking speed and activity. Thus the rate of departure is independent of prey or predator density, if it is true that when the predators arrive at the edge of a colony they make no distinct decision to leave or stay.
To test this hypothesis, simulations of the rate of departure were compared

Table 67. Walking behaviour of females of two phytoseiid species in presence and absence of prey and predators in the webbed area.

Predator species	Prey density (number/ cm^2)	Number of predators	Walking speed (mm/s)	Walking activity (%)	Simulated linear displacement after 200 steps (number of steps)
Phytoseiulus persimilis	0	1	0.19	12	45
	20-60	1	0.19	8	43
	20-60	4	0.20	9	44
Metaseiulus occidentalis	0	1	0.18	40	32
	20-60	1	0.20	36	29
	20-60	4	0.20	38	29

with measurements of the actual rate of departure from a colony. Three kinds of colonies were used:

- small webbed areas without prey, founded by males and preoviposition females
- large webbed areas without prey, founded by males and preoviposition females
- large webbed areas with prey eggs only, founded by ovipositing females, which were removed before the experiment.

Such a colony was located on one leaflet of a composed leaf and to provide an alternative residence for the predator, one or more of the other leaflets were also colonized with Type 3 colonies. One female predator was released on the upperside of a leaflet containing the adequate kind of colony After the predator invaded the colony, the residence time was registered by continuous observation (i.e. 14 hours per day) over a period of 3 days. The departures were scored after detection of the predator in the act or after discovery of the predator in one of the alternative colonies. The mean distance walked to reach the edge of a circular colony was computed from 100 Monte Carlo simulations of the walking pattern, and this estimate was converted into the residence time using the walking speed, the walking activity and, if prey was present, the feeding time. The residence times estimated from the experimentally defined walking behaviour correspond with the directly measured residence times, as long as the prey was absent (Table 68). Therefore it can be concluded that the residence time in the webbing is determined by the low walking velocity, the low walking activity and the tortuous walk. Probably surface enlargement, walking impedement and the increased frequency of tactile probing before advancement in the heterogeneous web structure are the factors determining the residence time in the webbed

Table 69. Rate of departure by young female phytoseiids from a colony in relation to prey density. T = 20°C; RH = 70%; webbed area = 4-11 cm².

Predator species	Prey density (number/cm²)	Simulated relative gut filling (%)	Number of predators in the colony		Relative rate of departure ($hour^{-1}$)
			at the start $N_{t=0}$	after 10 hours $N_{t=10}$	
Phytoseiulus persimilis	40-60	92	24	24	0
	25-35	91	51	48	0.006
	10-15	88	38	20	0.064
	5-10	85	41	6	0.192
	0- 5	< 81	32	0	0.868
Metaseiulus occidentalis	40-60	92	45	44	0.002
	25-35	90	32	29	0.010
	10-15	87	36	16	0.081
	0- 5	< 80	19	0	0.977
Amblyseius bibens	30-40	91	30	30	0
	10-15	88	30	14	0.076
	0- 5	< 81	29	0	0.792

are given in Table 69 in relation to the density of the prey. Because the fraction of residing predators decreased in an exponential fashion, the dispersal tendency can be characterized by the relative rate of departure according to the following formula:

$$\mathrm{RRD} = \frac{-\ln(N_t/N_0)}{t}$$

RRD = relative rate of departure ($hour^{-1}$)

N_t = number of predators residing in the colony at time t (hours).

If possible, the RRD values were computed from the time elapsed until 50% of the predators had left the colonies. To provide some insight in the mean level of gut filling at the different density classes, simulated values of the relative food content of the gut are given.

The results demonstrate the dependency of the rate of departure on prey-egg density while interspecific differences seem to be absent. As prey density decreases, the rate of departure increases. This effect cannot possibly be explained by a decreased time expenditure in feeding activities. Even for the extreme case of 16 egg captures in the 10 hour period (*Phyto-*

seiulus persimilis), the total feeding time would amount to 1 hour. The residence times are therefore predominantly determined by the walking behaviour at the edge of the colony, as argued in the previous subsection. Finally it is a glaring fact, that at the density of 10-15 eggs per cm^2 half the initial number of predators had left their colony after 10 hours, although their gut filling was still rather high according to the computations.

This high rate of departure may be due to the absence of female spider mites in the experiments. Hence the experiment has been repeated for the prey density of 10-14 eggs and 0.5 female per cm^2. Despite the inevitable oviposition by the female spider mites prey-egg density remained within the limits indicated. The results (Table 70) show that the additional presence of the female spider mites did not alter the rate of departure. Hence it may be supposed, that prey density is the governing factor in the realization of the residence time of the female predators.

Evidently there is a strong tendency to forage at densities above 20 eggs per cm^2. Natural selection may have favoured this dispersal behaviour as a consequence of the achievement of a larger progeny, but this simplified explanation is not clear, as long as the energy expenditure involved in reaching other more favourable food areas is not known. It may as well have been evolved as an anticipation on the survival chances of their progeny. The experiments, discussed in Subsection 2.2.1, demonstrate, that development was retarded and mortality was increased below a food supply of 1-2 eggs per day. However the assessment of juvenile dispersal yielded only some accidental departures at this critical rate of food supply and even unfertilized females had a low tendency to disperse (Table 71). Because the density of phytoseiid eggs can rise above the level of 1 egg per cm^2 colonized area

Table 70. Rate of departure by young female phytoseiids from a prey colony containing eggs and females. T = 20°C; RH = 70%; webbed area = 6-10 cm^2; 10-14 eggs/cm^2 and 0.5 female spider mite/cm^2.

Predator species	Number of predators in the prey colony		Relative rate of departure (hour^{-1})
	at the start $N_{t=0}$	after 10 hours $N_{t=10}$	
Phytoseiulus persimilis	30	16	0.063
Metaseiulus occidentalis	42	23	0.060
Amblyseius bibens	28	17	0.050

Table 71. Rate of departure from a prey colony by juveniles and unfertilized females of two phytoseiid species. *T = 20°C; RH = 70%; webbed area = 4-11 cm²;* prey egg density = 1-3 eggs/cm².

Predator species	Predator stage of development	Number of predators in the colony	
		at the start $N_{t=0}$	after 10 hours $N_{t=10}$
Phytoseiulus persimilis	larva	51	49
	protonymph	24	23
	deutonymph	41	39
	unfertilized female	37	35
Metaseiulus occidentalis	larva	10	10
	protonymph	28	26
	deutonymph	43	41
	unfertilized female	32	30

(Part 2), it is not unrealistic to suppose a profitable effect of the dispersal behaviour of the adult female predators on the developmental prospects of their less migratory juvenile progeny. This question will be investigated further by sensitivity analysis of the population model with respect to the relative rate of departure (Part 2).

3.4.3 Predator density

Kuchlein (1966) measured an increased tendency of young females of *Metaseiulus occidentalis* to disperse from the experimental leaf discs when more than one predator was present per area; predators leaving the disc drowned in the water-soaked cotton surrounding the disc. Kuchlein stated that the data on migration tendency thus obtained are of arbitrary value as long as a similar study of the dispersal on an actual plant is lacking. An experiment to provide this information will now be described.

The experimental procedure differs from that discussed in the previous subsection in the following respects. One, two or four females of *Metaseiulus occidentalis* were released on the leaf system instead of only one. Because the predators were allowed to invade the colony on their own accord, the colonies were frequently occupied by a lower number of predators than released on the leaf. Only colonies that contained adequate (1, 2, 4) numbers of predators were selected. The departures were assessed at consecutive time intervals of 4 hours by detection of the predator in one of the alternate colonies on the other leaflets of the rose leaf. When a predator left the

Table 72. The relative rate of departure of young females of *Metaseiulus occidentalis* related to predator density. T = 25°C; RH = 65%.

Initial number of predators invaded in the colony	The range of prey egg densities	Relative rate of departure (hour^{-1})			
		first assessment	after one departure	after two departures	after three departures
4	10-20	0.202	0.113	0.074	0.039
2		0.033	0.017	-	-
1		0.027	-	-	-
4	20-40	0.133	0.096	0.048	0.022
2		0.016	0.010	-	-
1		0.028	-	-	-

colony it was removed to prevent re-invasions; the observations were continued for the remaining predators until all were gone or until the experimental period, of 24 hours, had elapsed. This experimental procedure was carried out at two levels of prey density: 10-20 eggs per cm^2 and 20-40 eggs per cm^2. The predator densities were biased due to variation in the webbed areas per colony ($\hat{\mu}$ = 6.2 cm^2, $\hat{\sigma}$ = 3.1; range: 3-14 cm^2), but this variation was present for each level of predator release. The values of the relative rate of departure, each computed from an initial amount of at least 100 predators, are given in Table 72. As predator density decreases during the experiment as a consequence of the departures from the prey colony, the relative rate of departure was computed for each 4-hour period, thereby classifying the replicates with respect to the predator density at the start of these periods. In this way it was possible to calculate the RRD-values after one, two or three departures in case four predators were initially present in the prey colony and, similarly, after one departure in case two predators were initially in the colony.

Evidently there is a tendency to avoid predator aggregation even for high prey densities. This can be recognized from the data in two ways. First, the relative rate of departure increases for an increase in the number of predators initially present in the colony. Second, each departure is followed by a period with a lower value of the relative rate of departure. These tendencies are very similar at both levels of prey density. Also, the higher dispersal at the lower density range confirms the findings discussed in the previous subsection. For some reason (e.g. differences in temperature, distribution of prey densities within the class range) the RRD values obtained after the one predator release are higher than those stated in the preceding subsection.

4 The use of experimental and theoretical results in dynamic population models

The preceding chapters of this Agricultural Research Report describe the modelling of an acarine predator-prey interaction at the individual level and the measurements of the input data needed for that modelling; four species of phytoseiid predators were studied in relation to their prey, the two-spotted spider mite, which feeds on greenhouse roses. The results of these laboratory studies at the individual level are to be used for the modelling of the predator-prey interaction at the population level in the greenhouse. Because of this extrapolation to the population level it is worthwhile to realize which assumptions underlying the predation models are still unvalidated, and which input data are still missing. In addition, some important questions arise that are based on the available experimental evidence at the individual level; these will have to be solved by experiments and simulations at the population level. The unvalidated assumptions, the missing inputs and the questions that relate to the population level are considered in this chapter, preparing the way for Part 2 (to be published) of this report, which deals with the modelling of the predator-prey interaction at the population level.

4.1 UNVALIDATED ASSUMPTIONS

In Chapter 3, models have been developed for the simulation of the walking behaviour and the rate of predation of phytoseiids. These models were used for the analysis of the predator-prey system at the individual level. The results are to be used in the population models presented in Part 2. Some of the assumptions underlying these models are based on meagre experimental evidence; others have no empirical basis at all.

Though the Queueing model of the predation process proved to be as good as or even better than other predation models and successfully simulated the rate of predation under various conditions (Section 3.3), it should be remembered that it rests on four basic assumptions, each of which needs separate validation. First, a Poisson distribution is assumed for the number of prey captures per unit time at a certain level of the motivational state of the predators. Second, the food content of the gut is assumed to determine the state dependent rate of successful encounter, whether this state is achieved by previous gut emptying or by previous ingestion of food. Third, it is assumed that the food quality of prey is the same for all prey stages. This assumption is implicitly made since the flow of ingested food is merely treated in terms of weight. Some attempts have been made to validate the assumption by considering the available data of predation and reproduction rates in monocultures of diverse prey stages, but they did not provide any decisive evidence (Subsection 3.1.3). Fourth, the model of the predation process is based on the assumption that the state dependent success ratios measured in 'monocultures' of each prey stage are also applicable in 'mixed cultures' of several prey stages (Subsection 3.3.7); the probability of a prey capture after prey detection merely depends on the level of gut filling and past experience in capturing other prey stages is only registered via changes in the level of gut filling. This assumption is not refuted by the available experimental evidence, but more validation experiments are still needed.

Another point for comment is the concept of food conversion, which is basic to the population model of the predator-prey interaction. The present status of the systems analysis points to the important role of the relative rate of food conversion in determining the rate of predation at various temperatures, different oviposition histories, and prey and predator densities (Section 3.3). The increase in the rate of predation with increasing temperature is determined not by temperature-related changes in the searching behaviour, but by the effect of the temperature on the relative rate of food conversion into egg biomass. The relative rate of food conversion is shown to depend on the number of eggs already deposited by the female predator, i.e. its oviposition history. However, only circumstantial evidence was given for the assumption that the decrease of the rate of predation at increasing predator density is caused by a decrease in the relative rate of food conversion, and not by behavioural changes of the predators after mutual contact, nor by the time wasted for prey searching upon mutual contact between the predators. Furthermore it should be recalled that the food content of the gut is not a good indicator of the motivational state when the predator is severely starved (Subsection 3.1.2 and 3.2.7)

Simulations of experimentally defined walking behaviour were carried out to determine the effect of recrossing areas already searched by the predator on searching efficiency, and to estimate the residence time in a circular webbed area under the assumption that the edge of the webbed area exerts no effect on walking behaviour. These simulation experiments show that the tortuous walk of the predatory mites in the prey colony leads to an approximately 20% decrease in the rate of encounter with immobile prey (Subsection 3.2.4), and that the predator cannot stay in a profitable prey patch but by turning at the edge of the webbed leaf area (Subsection 3.4.1). However, the walking paths simulated on the basis of experimentally determined parameters (μ, σ, λ and α_m) were not explicitly tested for goodness of fit, though with the naked eye the simulated paths were indistinguishable from the paths originally measured. The auto regression model of the walking process was the best available model to comprehensively describe the characteristic properties of the walking pattern (Subsection 3.2.4). Anyway, the simulated level of recrossing is low and is hardly affected by even 20% changes in the parameter values. Moreover, long residence times in a profitable prey patch are best explained by the edge-turning strategy; without the edge effect simulated residence times equal to those determined experimentally could only be obtained for extreme types of walking behaviour that differ largely from the measurements at naked eye inspection. Hence prey density predominantly determines the relative rate of departure of the predator from the prey colonies that will be generated by the model at the population level.

4.2 MISSING INPUTS

In Chapters 2 and 3 experiments with individual mites have been described that serve to measure rate variables for use in population models. For some cases the set of inputs is incomplete, or the results cannot be used in the population models without making new assumptions, which in turn need separate validation. To gain insight into these limitations it is worthwhile to look at these aspects in more detail.

The possibility of maintaining a predator population in periods of prey scarcity in the greenhouse is of considerable practical importance; it would be convenient if the predators residing in the crop are able to detect new spider mite infestations in due time for control of the mite pest. Literature data and some additional experiments have provided some insight into the survival chances of the predatory mites in the greenhouse. When prey is scarce in the greenhouse rose crop, the availability of water seems to be most important for the survival of the phytoseiids (Subsection 2.2.5). Cannibalism provides only a limited means for survival, as it depends on the survival of other predators, and as the food and moist content of these predators decreases exponentially with the length of food deprivation (Subsection 2.2.6). The supply of pollen on the rose plants did not improve survival in comparison to the supply of water only (Subsection 2.2.7). However, because only one level of pollen supply was tried, no decisive, practical information can be given on the possibility of maintaining a predator population in the rose crop. Anyway, the amount of pollen originating from the flowering roses in the greenhouse is insufficient in this respect. At higher levels of pollen supply, especially *Amblyseius bibens* may perform better, as shown by Blommers (1976) in small scale experiments.

By extrapolating data on individual life histories measured at constant temperatures to the greenhouse situation, an important assumption is made that has been only partially validated. The rate of development, the rate of reproduction, the rate of mortality, the rate of webbing and the rate of predation were measured at constant temperature levels in the range 10-35°C. Of course, temperature will fluctuate in the greenhouse albeit within limits

(10-35°C). The effect of variable temperature regimes on these rates was investigated for the two-spotted spider mite, but hardly at all for the phytoseiids considered in this report. But because the population model presented in Part 2 is based on the assumption that birth, death and predation processes react instantaneously to changes in temperature, validation of this assumption is still needed for the phytoseiids.

Though the prey supply to the predators has been quantified in such a way that prey density and prey number can be computed in the population model (Part 2), the level of food supply to the spider mites has not been considered. Some arguments have been given to consider the nutritional value of the host plant as a constant for spider mites infesting greenhouse roses (Section 2.1). However, in contrast to the food quality of the rose leaves, food quantity can be affected by feeding of the spider mites themselves. The available leaf parenchym decreases during population growth of the spider mites until the host plant is exhausted as a food source, or the grower applies pesticides. Also, the juvenile spider mites are left stranded in already exploited areas, because they are less able to disperse. As the life history variables have been measured for individual spider mites and plenty of fresh plant food, an important gap in the experiments may be present. Therefore, to decide if these factors need to be studied in more detail, a greenhouse experiment on population growth of the spider mites should be carried out and the numerical results should be compared with simulations that neglect the effects of competition for food among the individual spider mites. This population experiment and the adherent simulations will be discussed in Part 2.

Another subject that is important in the interpretation of the results of population simulations is the determination of the sex ratio. Although the sex ratio of the progeny can depend on arthropod-related factors, such as the age of the spider-mite 'mother' (Subsection 2.1.3), it is assumed to be a fixed ratio that does not alter in response to environmental conditions. But this is an assumption made because of lack of experimental data, rather than a well-established foundation for population modelling. Control of the fertilization process and hence the sex ratio in response to environmental conditions may play a role in arthropods reproducing by arrhenotoky. This possibility should be taken into consideration when interpreting the sex ratios simulated and measured at the population level (Part 2).

An important state variable in the population model of the predator-prey interaction is the prey density. In this report the prey density is defined as the number of prey per square centimetre of webbed leaf area, because two-spotted spider mites *only* inhabit those parts of the leaf area covered by webbing. During population growth not only do prey numbers increase, but also the extent of the webbed area. Therefore, for calculation of prey density for simulations at the population level, life history components, as well as the rate of increase of webbed leaf area, have been measured at the individual level (Section 2.1). The rate of increase of webbed leaf area can depend on the host plant species that is colonized by the two-spotted spider mite. For example, the webbing cover on Lima bean is less aggregated than on rose, and the webbing is even more spread out on leaves of Gerbera. Presumably the hairiness of the leaves is an important factor in this respect. The rate of colonization estimated in this study on rose 'Sonia' is therefore by no means generally applicable and should be determined for other plants.

By distinguishing webbed leaf areas from unwebbed leaf areas it is necessary to assess which factors determine the residence time of the predators inside and outside the webbed area. The residence time of individual predators in the webbed area of a prey colony has been studied in this report, but their residence time outside the webbed area is an aspect that has not yet been considered fully at the individual level. Some details have been discussed in Subsection 3.2.4 and 3.4. It was found that the predatory mites walk along the leaf edge or a rib, invading the prey colony after making tarsal contact with the silk strands attached to the leaf edge or rib. *Amblyseius potentillae* behaved differently. This phytoseiid predator tends to avoid the webbed leaf area and prefers to stay next to the thick parts of the main rib of a rose leaf or at other protected spots on the plant. More knowledge is required on the question of how a predatory mite searches for new prey patches, especially how the searching is influenced by the mode of plant or crop colonization by the two-spotted spider mites. These aspects will be discussed in Part 2 of the Agricultural Research Report.

4.3 IMPACT OF INDIVIDUAL CHARACTERISTICS AT THE POPULATION LEVEL

The measurement of mite properties at the individual level can sometimes be sufficient for the evaluation of their impact on the population level. For example, hatching of phytoseiid eggs fails for relative humidities of 30-60%, but the spider mite eggs are not affected in this range. Hence egg mortality is probably a key factor in the failure of phytoseiids to control the population growth of the two-spotted spider mites at low humidities. In other cases, the measurement of mite properties at the individual level is not sufficient for the evaluation of their relative importance at the population level. For example, what is the importance of a 10% shorter developmental time relative to a 10% rise of the rate of reproduction? Both developmental time and reproduction affect the rate of population increase, but their relative effect cannot be determined without the help of a quantitative tool, such as a mathematical model of the population growth. The evaluation of such effects is even more difficult when their relative importance has to be assessed for interacting populations of predator and prey. Hence the evaluation of the interspecific differences in life histories is deferred to Part 2, where the predator-prey interaction is modelled at the population level.

Because several processes in the predator-prey system interact with each other, and several rate variables depend in a non-linear way on state variables, it is often not possible even to describe the consequences of input data measured at the individual level for the interaction at the population level, let alone to indicate their relative importance. The role dynamic simulation may play in this respect is further illustrated in three examples.

Example 1 - the role of webbing in predation The searching behaviour of individual female predators has been studied in the webbed leaf area, as well as on unwebbed leaves (Section 3.2). Webbing interferes generally with searching by decreasing the rate of encounter per unit prey density (the relative rate of encounter), as a consequence of a reduction in the walking speed, the walking activity and the coincidence between predator and prey in the webbed space. The relative rate of successful encounter was affected by the webbing in different ways, however, depending on the phytoseiid species involved: the success ratio of *Phytoseiulus persimilis* increases in the presence of webbing; the success ratios of *Amblyseius bibens* and *Metaseiulus occidentalis* are unaffected by the webbing; but the success ratio of *Amblyseius potentillae* decreases (Subsection 3.2.7). It is shown by simulation of the predation rate on basis of these behavioural data, and the dynamics of the gut filling, that the increase of the success ratio of *Phytoseiulus persimilis* in the webbing more than compensates for the reduction of the relative rate of encounter in the webbing, resulting in an increase in the rate of predation in a prey colony (Subsection 3.3.3). The factor webbing may therefore be important for future studies of the interaction between phytoseiid predators and the two-spotted spider mite, but the relative importance of the substrate-related differences in predation rate has yet to be demonstrated at the population level (Part 2).

Example 2 - prey-stage preference of the phytoseiid predators The probability of capturing a prey depends very much on the prey stage involved (Subsection 3.2.7): eggs are easier to capture than larvae, larvae are more easy to capture than nymphs and the adult female spider mites are the most difficult to capture. These prey-stage specific differences in success ratio may mean that the diet of the predator largely consists of the young prey stages and that the reproductive spider mite females are allowed to continue the reproduction process for some time. Hence the extermination of the prey population may be postponed due to the initial concentration of the predators on the young prey stages. On the other hand, the adult female spider mites do not live for ever and each consumption of a female juvenile prevents the development of a reproductive female. Therefore the hypothesis that predators keep 'laying hens' should be evaluated by dynamic simulation of the predator-prey interaction at the population level (Part 2).

Example 3 - dispersal of the predator from colony to colony When female predators tend to stay in colonies with high prey densities, this tendency can lead to predator aggregation in the profitable prey patches, which in turn leads to a decreased rate of predation (and thus reproduction), *or* to predator dispersal from the prey patch (Section 3.4). What effect this mode of prey patch exploitation has on the population level is an important question that may be solved by dynamic simulation of population growth and dispersal. For these simulations, where predators may move from one prey colony to the other, possibly differing in prey density, and where prey density continually changes in time, it is necessary to account for the non-steady state of the predation process. The Queueing model developed in Chapter 3 offers that facility and, moreover, it can be easily coupled to a population model in the form of a subroutine.

Summary

The two-spotted spider mite, *Tetranychus urticae* (Acarina: Tetranychidae), is a major pest of many food and ornamental crops. In the greenhouse culture of ornamental roses, an acaricide, called dienochlor [perchlorobi(cyclopenta-2,4-dienyl)] is used to control it. For environmental reasons it is desirable to replace chemical spraying with a better alternative. This Agricultural Research Report describes investigations into the possibility of biological control of two-spotted spider mites in greenhouse roses with predatory mites (Acarina: Phytoseiidae). Biological control has been successful in the greenhouse culture of cucumbers, for example. In greenhouse roses, however, much less damage can be tolerated because the ornamental value of their flowers and leaves determines the economic value of the crop. This quality demand applies especially to the rose shoots that grow above the rose hedge, which are cut off at a beginning stage of flowering; more damage can be tolerated in the rose hedge itself. Spider mites should be controlled in such a way that damage to the young rose shoots is minimized.

Two-spotted spider mites are able to double their number in the short period of 2-4 days. Even after the release of the predatory mites the population of spider mites will increase initially. Only after some time will it decrease. Hence it is important to estimate the minimum number of predators to be released for acceptable mite control. The control of newly developed infestations will depend on the ability of the phytoseiids to survive periods of prey scarcity. Because phytoseiid species can differ in their ability to survive or reproduce on alternative food, and in their predation capacity, four species are compared with each other, i.e. *Phytoseiulus persimilis*, *Amblyseius potentillae*, *Amblyseius bibens*, *Metaseiulus occidentalis*.

The potential role of these predatory mites for the control of the two-spotted spider mites has been investigated by systems analysis, i.e. by modelling and experimentation. In this Agricultural Research Report, experiments and models at the individual level are considered. In Part 2 of this report (to be published) the results of these experiments and models will be used in a new model to simulate population growth of both predator and prey; simulations with this population model will be compared with population experiments in the greenhouse. After validation the model can be used for calculation of the minimum release of predatory mites at a certain stage of pest development. These estimates may then be transformed into simple rules of thumb.

For a systems approach it is necessary to quantify the prey supply (in

particular, two-spotted spider mites) to the predatory mites in the greenhouse. Because the spider mite numbers increase with time, the properties of tetranychids were investigated that determine the rate of population increase, i.e. the developmental time, age-dependent reproduction and the proportion of females in the progeny (Subsections 2.1.1-2.1.3). Environmental temperature influences the rate of development and reproduction of poikilothermic arthropods. It was shown that the relation between temperature and these rates is linear in the range 12-35°C; under greenhouse conditions relative humidity is not important. Furthermore, it was shown that the rate of reproduction and the proportion of the progeny that are females depends on the age of the reproductive female. With respect to the quantification of the prey supply to the predators, it is also important to distinguish the stages of development, because each stage runs different risks of being captured by the predatory mites. Hence the rate of mortality and development were measured for each developmental stage, so that in population simulations the prey supply can be subdivided per prey stage.

The prey supply to the predator is also determined by the mean distance between prey items, i.e. the prey density. Two-spotted spider mites have a strong tendency to aggregate. They construct labyrinths of silk strands on the lower side of the leaf, starting from the leaf edge or a rib and dispersing over the leaf surface. In the webs, the eggs are deposited and develop into adults. The preoviposition females are inseminated immediately after the last moult and subsequently disperse, frequently to other leaves, where they form new colonies. Hence colonization is an essential aspect of the prey supply to the predator. The predatory mite has to invade the webbing to capture its prey. Therefore the prey supply is defined as the number of spider mites per square centimetre webbed leaf area. Consequently, the rate of increase of webbed area was quantified by experiment (Subsection 2.1.6). On the basis of the measured rate of webbing and the measured life-history components, a population model can be constructed that simulates prey numbers *and* prey density in the course of the predator-prey interaction (Part 2).

In the greenhouse culture of ornamental roses, food substances other than spider mites are rare. Hence the survival of the predators in periods of prey scarcity will depend on cannibalism and abiotic factors, such as the availability of water, temperature and relative humidity. In contrast to the other phytoseiid species studied, *Amblyseius potentillae* and *Amblyseius bibens* can reproduce when feeding on pollen, so that the addition of these plant substances may lead to the maintenance of the predator population in the greenhouse crop. Experiments indicate that the amounts of pollen required are probably high (Subsection 2.2.7). Honey and sucrose solutions can improve the rate of predator survival to a significant extent. To date the possibility of maintaining a predator population in a rose crop without spider mites has still not been demonstrated.

Population growth of the predatory mites will depend on the number of spider mites in the webbed leaf area and the temperature and relative humidity there (Subsections 2.2.1-2.2.3). As for the spider mites, the rate of development and the rate of reproduction are linearly related to temperature. However, when temperature rises above 30°C and relative humidity drops below 70%, juvenile mortality becomes high. As the spider mites are much less vulnerable to temperatures in the range 30-35°C and humidities in the range 40-70%, these conditions are critical for their control by predatory mites. The four phytoseiid species studied differed with respect to developmental time, size of progeny and proportion of females in the progeny. However, all phytoseiid species matured in a shorter time-span, but laid fewer eggs than the two-spotted spider mites. The relative importance of these differences can not be determined without the help of a quantitative tool, such as a population simulation model. The evaluation of these differences will therefore be treated in Part 2 of this Agricutlural Reseach Report.

When prey supply is sufficient, young phytoseiid females utilize approximately 70% of the ingested food for egg production. In addition, the rate of oviposition is so high that the reproducing females determine the predation capacity of the phytoseiids. The rate at which the ingested food is utilized for egg production of new protoplasm was found to be mainly dependent on the individual oviposition history, that is to say on the number of eggs already deposited by the female predator; female predators tend to achieve potential fecundity almost irrespective of their age. Hence the reproductive females represent the most voracious stage of the predatory mites, and they decide where and when the eggs are deposited. For this reason the searching behaviour of the female predators was studied in an attempt to relate prey supply to predation and, consequently, reproduction (Chapter 3).

For a study of the searching behaviour it is important to characterize the motivational state of the predator. Since the rate of food conversion is high, it makes sense to use the food content of the gut as an indicator of the motivational state of the predator. The dynamics of the gut filling can be computed when ingestion, resorption and egestion are quantified by experiment. By weighing hungry predators before and after food intake the food content of the different prey stages, the gut content and the food deficit of the gut were measured (Section 3.1). Likewise, it was possible to quantify the rate of ingestion and the rate of gut emptying. These data were used in a model of food conversion that is based on the assumption that the surplus of the resorbed food substances is used for egg production (Fig. 21). This model was tested, for example by computing the time needed for a hungry female to produce an egg. The calculations were correct in a broad range of food deprivation periods, but after a certain period of food deprivation a period of recovery was necessary before the female restarted egg production.

The food conversion model (Appendix A) was used for the analysis of the observations of the predatory behaviour. Young female predators belonging to four different species of Phytoseiidae were deprived of food for some specified period, starting from a state of satiation, and then placed in a prey colony. Their behaviour was recorded and the dynamics of the gut filling computed. Thus it is possible to relate walking velocity, walking activity, walking pattern, success ratio and feeding time to the estimated level of food in the gut of the female predator (Section 3.2).

This experiment was carried out on two substrates: webbed leaf and unwebbed leaf. It was therefore possible to assess the role of webbing in the searching behaviour of the predatory mites. In the webbing the rate of encounter per unit prey density was found to be lower, because predatory mites, as well as spider mites, move slowly on this substrate and spend less time in walking. The slow advancement of the mites prevents bumping of one mite into another, so that disturbance of the predator is a rare phenomenon. On an unwebbed substrate disturbance is important, as is reported by several authors. The coincidence between predator and prey and hence also the rate of encounter are lowered as a consequence of the labyrinth formed by the webbing: predator and prey may move over and under each other without encountering one another. The predatory mites probably search at random and locate their prey after contact with the tarsi of their front legs (Subsection 3.2.3). However, not every encounter leads to a successful attack. It was shown that the success ratio depends on the gut filling of the predator, the prey stage and, in two specific cases, on the substrate: in the webbing the success ratio of *Phytoseiulus persimilis* increases and that of *Amblyseius potentillae* decreases (Subsection 3.2.7, Fig. 33).

The results of this behavioural component analysis were used in a predation model derived from queueing theory (Section 3.3). This theory has been used in problems concerning waiting-lines of customers and service facilities. Consider, for example, a queue of patients in a dentist's waiting-room. The patients represent the prey, the dentist represents the predator and the waiting-room represents the gut of the predator. The rate of patient arrival in the waiting-room is equivalent to the rate of predation; the time needed to help the patient is equivalent to the time needed to empty the gut of the predator by the amount of one prey. As more patients enter the waiting-room, the dentist will shorten the consulting time per patient and it becomes increasingly probable that newly arrived patients will refuse to wait and decide to return at another time. Analogous to this example, the rate of gut emptying increases with an increasing level of gut filling, and, simultaneously, the motivation of the predator to attack its prey decreases, while the probability of prey escaping increases. Both tendencies were demonstrated by experiment.

A stochastic queueing model can be derived if one assumes that the number of successful attacks by a predator with a certain level of gut filling fits a Poisson distribution and that the gut emptying time per ingested prey is distributed according to the negative exponential distribution. This model was compared with a deterministic model, a Compound simulation model and a Monte Carlo simulation model of the predation process (Appendices E-H). The Queueing model is preferred because of its economic use of computer time and because it uses a minimum number of variables without losing precision (Subsection 3.3.1).

The Queueing model was validated in a series of predation experiments carried out on webbed and unwebbed leaves (Subsections 3.3.2 and 3.3.3). The rate of encounter per unit prey density is lowered by the presence of webbing, which results in a decreased rate of predation for *Amblyseius bibens* and *Metaseiulus occidentalis*. Opposed to this decrease in searching ability, the prey density in the webbed area is high (20-60 mites per square centimeter of webbed leaf area). So the rate of encounter between predator and prey turns out to be high, anyway. According to the simulations, *Phytoseiulus persimilis* and *Amblyseius potentillae* are affected by the webbing in a similar way, but the probability of these predators capturing a prey after tarsal contact (success ratio) is strongly influenced. *Amblyseius potentillae* has a lower success ratio in the webbing than on unwebbed leaves, and this results in an extra decrease of the rate of successful attack. In contrast, *Phytoseiulus persimilis* has a higher success ratio in the webbing, which more than compensates for the decrease of the searching ability (= the rate of encounter per unit prey density): the rate of predation in the prey colony is higher than on unwebbed leaves with the same number of prey per leaf area.

Systems analysis of the predation process at different levels of the temperature shows that the effect of temperature on the rate of food conversion determines the rate of predation (Subsection 3.3.4). Behavioural changes related to temperature are probably of minor importance for the increase of the rate of predation with temperature. Presumably the decreased rate of reproduction at increased predator densities is also caused by a decrease in the rate of food conversion, and not by changes in the searching behaviour or by an increase of the time wasted during mutual contact between predators (Subsection 3.3.6). Because female phytoseiids tend to achieve their potential fecundity, it is supposed that the rate of food conversion as well as the rate of reproduction is not dependent on age but on the number of eggs deposited by the female (Subsection 3.3.5). In conclusion, the rate of food utilization for egg production is probably the most important factor in determining the rate of predation, and the ability to capture prey can probably be considered as a constant related to a specified substrate.

Finally the Queueing model was extended to the case of 'mixed cultures' of prey stages (Subsection 3.3.7 and Appendix I). The preference for each specific prey stage is determined in the model by success ratios, which were measured in 'monocultures' of these prey stages. These measurements show that spider-mite eggs are easier to capture than larvae, that larvae are easier to capture than nymphs and that the adult female spider mites are the most difficult to seize. Moreover, they show that the differences between success ratios of the different prey stages become smaller as the gut filling of the predator decreases: the predator is less fussy as its hunger increases. Simulation and measurement of predation in mixed cultures of larvae and adult females of the prey suggest that the 'monoculture' success ratios sufficiently describe the probability of capture under these circumstances. More validation experiments are needed, however.

The residence time of a predator in a prey colony is mainly determined by the prey density (Subsections 3.4.1 and 3.4.2). This is evident from the comparison of the residence time of predators in webbed areas with and without prey. Analysis of the walking pattern of the predatory mites in the webbing and, based upon this analysis, simulation of the residence time in the webbed area shows that the tortuous walking path of the predator does not explain the length of the residence time in the prey colony. The experimentally measured residence times in prey colonies can only be achieved by the predator when it turns back at the edge of the colony. The simulation of the walking behaviour of the predator shows that it comes in contact with the edge frequently enough to react adequately to a decreasing prey supply. When female predators stay in colonies of high prey density, predator density may increase there. It was shown by experiment that an increase of the predator density leads to a shorter residence time despite the ample supply of prey (Subsection 3.4.3). Hence predator and prey density are the major factors determining the residence time of the predatory mites in a prey colony.

In distinguishing webbed leaf areas on the plant from unwebbed ones, it is not sufficient to determine only the factors that regulate the residence time in the prey colony. It is also necessary to find the factors that determine how much time is spent outside the prey colonies: how does a predatory mite search for new prey colonies? Of course, this is also an aspect of the analysis at the individual level, but it will be discussed in Part 2 of this report in relation to the colonization of the plant by the spider mites. Some details, however, have been discussed in Subsection 3.2.4 and Section 3.4. It was found that the predatory mites walk along the leaf edge or a rib and that they invade the prey colony after making tarsal contact with the silk strands attached to the leaf edge or the rib. *Amblyseius potentillae* behaves very different in this respect. This phytoseiid predator tends to avoid the webbed leaf area and prefers to stay near to the thick parts of the main rib of a rose leaf or other protected 'holes and corners' on the plant.

The measurements at the individual level give rise to questions which can be solved only by simulation and experimentation at the population level (Chapter 4). An example is the measurement of the rate of departure of the predator from a prey colony at different prey and predator densities. What is the role of this dispersal mechanism in the population dynamics of predator and prey? As the number of mites and the colonization pattern are continuously subject to change, dynamic simulation in combination with population experiments in the greenhouse may provide the answer. This systems approach may also be useful in detecting missing knowledge on the individual level of the predator-prey interaction. For example, the rate of development and reproduction of the spider mites were measured for ample supply of food. Because the spider mites feed on the contents of the leaf parenchym, food quality may decrease and possibly the life-history variables are affected. If this is so, simulated population growth will exceed the measured population growth in the greenhouse. Population models can thus be used to elucidate the role of certain measured properties of predator and prey and to determine which experiments at the individual level may still be necessary to improve the existing population models.

Samenvatting

De kasspintmijt, *Tetranychus urticae* (Acarina: Tetranychidae), vormt een belangrijke plaag in een groot aantal voedings- en siergewassen. In de sierteelt onder glas wordt het kasspint chemisch bestreden met behulp van een gechloreerde koolwaterstofverbinding die bekend is onder de naam Pentac. Het is wenselijk om deze bestrijdingsmethode te vervangen door een milieuvriendelijk alternatief. Mijn onderzoek is erop gericht om mogelijkheden voor biologische bestrijding van het kasspint met behulp van roofmijten (Acarina: Phytoseiidae) te onderzoeken, en wel in de teelt van kasrozen. Deze methode wordt reeds met succes toegepast in de komkommerteelt en andere teelten van kasgroenten. Het probleem van de toepassing in de teelt van kasrozen is echter, dat hier veel minder zuigschade van het kasspint kan worden getolereerd, omdat het blad sierwaarde heeft. Deze hoge kwaliteitseis geldt voor de rozenscheuten die boven de rozenheg uitgroeien en in een vroeg stadium van de bloei worden afgesneden en verhandeld. Veel meer schade kan worden getolereerd in de rozenheg; het kasspint zal daar zodanig onder controle gehouden moeten worden, dat de jonge scheuten zo min mogelijk schade ondervinden.

De populatie van het kasspint kan zich in de korte periode van 2-4 dagen verdubbelen. Ook na het loslaten van de roofmijten zal de populatiegroei van het kasspint nog wel even doorgaan alvorens het aantal spintmijten zal dalen. Daarom is het van belang om te weten hoeveel roofmijten bij een bepaalde spintaantasting minimaal moeten worden uitgezet om een gewenst bestrijdingsresultaat te verkrijgen. Of de predatorpopulatie na onderdrukking van de plaagontwikkeling ook op eigen kracht nieuw opkomende spinthaarden de baas zal kunnen zijn, hangt af van haar vermogen om perioden van prooischaarste te overleven. De bepaling van dit vermogen is daarom van belang voor het inzicht in introductiestrategieën van roofmijten. Omdat verschillende roofmijtspecies verschillende combinaties van predatie- en overlevingscapaciteit bezitten, zijn een viertal soorten roofmijten met elkaar vergeleken, nl. *Phytoseiulus persimilis*, *Amblyseius potentillae*, *Amblyseius bibens* en *Metaseiulus occidentalis*.

Voor de oplossing van bovenstaande problematiek werd een systeemanalytische aanpak gekozen, d.w.z. combinatie van model en experiment. In Deel 1 van het rapport werden experimenten en modellen op het individu-niveau besproken. In Deel 2 (in voorbereiding) zullen de resultaten van deze individu-experimenten en de gevalideerde individu-modellen worden betrokken bij de constructie van een nieuw simulatiemodel, dat de populatiegroei van predator en prooi in tijd en ruimte berekent. De berekeningen met dit populatiemodel zullen vergeleken worden met populatie-experimenten in de kas. Pas na gebleken bruikbaarheid zal dit model kunnen dienen voor berekening van het minimale aantal los te laten predatoren bij een bepaalde spintaantasting en een bepaald wensenpakket van de tuinder. Wellicht kunnen deze schattingen dan voor de praktijk vertaald worden in vuistregels.

Voor de systeemanalytische benadering is het vereist om het voedselaanbod voor de roofmijten te quantificeren, te beginnen bij de kasspintmijten. Omdat het aantal spintmijten verandert in de tijd, werden eerst díe eigenschappen van de parenchymzuigende spintmijten onderzocht, die bepalend zijn voor de snelheid van populatiegroei, te weten: de ontwikkelingsduur, de leeftijdsafhankelijke reproductie en de geslachtsverhouding in het nakomelingschap (paragraaf 2.1.1-2.1.3). De omgevingstemperatuur speelt een belangrijke rol bij de ontwikkelings- en reproductiesnelheid van deze koudbloedige arthropoden. De relatie tussen de temperatuur en deze variabelen bleek in grote trekken lineair te zijn tussen 12°C en 35°C. Onder kasomstandigheden speelde de luchtvochtigheid geen belangrijke rol. De reproductiesnelheid en de geslachtsverhouding van het nakomelingschap bleken sterk af te hangen van de leeftijd van het reproductieve vrouwtje. De leeftijd van de juveniele spintmijt is ook van belang voor de kwantificering van het voedselaanbod voor de rovers, omdat de diverse ontwikkelingsstadia een sterk verschillende kans lopen om door een roofmijt te worden gevangen. Daarom werd de ontwikkelingsduur en de mortaliteit van elk ontwikkelingsstadium experimenteel bepaald, zodat het voedselaanbod in de simulatie van de predator-prooi interactie op populatie-niveau kan worden gedifferentieerd naar ontwikkelingsstadium.

Het voedselaanbod voor de predator wordt ook bepaald door de gemiddelde onderlinge afstand tussen de prooi-individuen, m.a.w. de prooidichtheid. Spintmijten vertonen een sterke neiging tot aggregatie. Zij huizen in een labyrinth van spinseldraden dat zij construeren aan de onderkant van het blad, beginnend langs de bladrand of de hoofdnerf en van daaruit expanderend over het hele blad. In deze spinsels worden de eieren gelegd en groeien de juvenielen op. De preovipositievrouwtjes worden onmiddellijk na de laatste vervelling bevrucht door de mannetjes en verhuizen dan veelal naar andere bladeren, waar een nieuwe spintkolonie wordt gesticht. Kolonievorming is dus een essentieel aspect van het voedselaanbod van de predator. Als de roofmijt spintmijten wil bemachtigen, zal deze de spinsels moeten binnendringen. Daarom werd het prooiaanbod voor de predator gedefinieerd als het aantal spintmijten per cm^2 bespinseld bladoppervlak en werd tevens de snelheid, waarmee individuele spintmijten bijdragen aan de bespinseling van het bladoppervlak, experimenteel bepaald (paragraaf 2.1.6). Met behulp van deze resultaten en de bepaling van de eigenschappen die de populatiegroei bepalen, zal een model worden geconstrueerd dat de prooiaantallen én de prooidichtheid in de tijd simuleert (Deel 2).

Naast spintmijten komen er in de teelt van kasrozen nauwelijks andere prooien of andersoortig voedsel voor. De overleving van de predatoren bij afwezigheid van spintmijten zal dus afhangen van de mogelijkheid tot kannibalisme en abiotische factoren, zoals de beschikbaarheid van water, temperatuur en luchtvochtigheid (paragraaf 2.2.5 en 2.2.6). In tegenstelling tot de andere onderzochte soorten kunnen *Amblyseius potentillae* en *Amblyseius bibens* reproduceren met pollen als voedsel, zodat toevoeging hiervan zou kunnen leiden tot handhaving van een predatorpopulatie. De benodigde hoeveelheden zullen waarschijnlijk groot zijn (paragraaf 2.2.7). Honing of sucrose-oplossingen kunnen de overlevingskansen van roofmijten aanmerkelijk vergroten. De mogelijkheden om in een rozengewas zonder spintmijten een predatorpopulatie te handhaven zijn nog niet aangetoond, maar vergroting van de overlevingskansen van een bestaande predatorpopulatie lijkt praktisch realiseerbaar.

De populatiegroei van de roofmijten zal afhangen van het aantal spintmijten dat zich op het bespinselde bladoppervlak bevindt, maar tevens van de temperatuur en de relatieve luchtvochtigheid (paragraaf 2.2.1-2.2.3). Ook bij roofmijten is de ontwikkelingssnelheid en de reproductiesnelheid lineair gerelateerd aan de temperatuur. Echter temperaturen boven 30°C en vochtigheden beneden 70% veroorzaken een hoge mortaliteit onder de juveniele roofmijten. Omdat spintmijten veel minder kwetsbaar zijn bij temperaturen tussen 30 en 35°C en bij lage luchtvochtigheden (40-70%), zijn deze omstandigheden in het kasklimaat kritiek voor de beheersing van spintmijtenplagen m.b.v. roofmijten. De vier onderzochte soorten roofmijten vertoonden onderling verschillen in ontwikkelingsduur, grootte van het nakomelingschap en de geslachtsverouding hiervan. Zij ontwikkelden zich echter allemaal sneller dan de spintmijten, maar legden minder eieren. De consequenties van deze verschillen zijn moeilijk te overzien zonder gebruik te maken van computermodellen van de predator-prooi interactie op populatie-niveau. De evaluatie van deze verschillen zal daarom in Deel 2 van dit rapport worden behandeld.

Als het prooiaanbod voldoende groot is, kunnen jonge roofmijtvrouwtjes ongeveer 70% van het opgenomen voedsel besteden aan de aanmaak van eieren. De eiproduktie is zo hoog, dat het voornamelijk de reproduktieve vrouwtjes zijn die de predatiecapaciteit van de roofmijten bepalen (paragraaf 2.2.4). De snelheid waarmee het voedsel wordt gebruikt voor de aanmaak van nieuw protoplasma bleek in hoofdzaak af te hangen van de ovipositiehistorie, d.w.z. het aantal reeds gelegde eitjes; roofmijtvrouwtjes lijken te 'streven' naar volledige realisatie van de potentiële eiproduktie. De reproduktieve roofmijtvrouwtjes zijn dus het meest vraatzuchtig en zij bepalen in welke kolonies de eieren worden gedeponeerd. Daarom werd het zoekgedrag van deze roofmijtvrouwtjes bestudeerd in een poging om het prooiaanbod te relateren aan de predatie en de daaruit resulterende reproduktie (Hoofdstuk 3).

Bij de bestudering van het zoekgedrag is het van belang om de motivatietoestand van de predator te karakteriseren. Gezien de hoge snelheid van de voedselconversie ligt het voor de hand om de voedselinhoud van de darm als indicator voor de motivatietoestand te kiezen. De dynamiek van de darmvulling kan worden berekend als de ingestie, resorptie en egestie experimenteel kunnen worden gekwantificeerd. Dit bleek mogelijk met behulp van een elektrobalans, waarmee het gewicht van individuele mijten kan worden bepaald. Door meting van het gewicht van een gehongerde roofmijt voor en na voedselopname kon de voedselinhoud van de verschillende prooistadia, de maximale darmvulling en het verzadigingsdeficit worden bepaald (paragraaf 3.1). Ook was het mogelijk om de ingestiesnelheid en de snelheid waarmee het voedsel uit de darm verdwijnt, te bepalen. Deze kwantitatieve gegevens werden gebruikt in een model van de voedselconversie, dat is gebaseerd op de aanname dat het surplus van de geresorbeerde voedingsstoffen wordt gebruikt voor de aanmaak van eieren (Figuur 21). Dit model werd op bruikbaarheid getest door bijvoorbeeld uit te rekenen hoeveel tijd een gehongerd roofmijtvrouwtje nodig heeft om weer een ei te produceren, en dit te vergelijken met experimenteel bepaalde tijdsperioden. De berekeningen bleken juist te zijn in een breed traject van hongerperioden, maar na een bepaalde hongerperiode veroorzaakte voedseldeprivatie effecten die om een herstelperiode vroegen alvorens het vrouwtje weer tot eiproduktie kon overgaan.

Het model van de voedselconversie (Appendix A) werd gebruikt bij de analyse van de gedragswaarnemingen. Jonge vrouwelijke predatoren die vanaf verzadigde toestand waren gehongerd voor een bepaalde periode, werden bij een prooikolonie geplaatst. Het gedrag van de predator werd geobserveerd en de dynamiek van de darmvulling werd berekend. Op deze wijze kon de loopsnelheid, de loopactiviteit, het looppatroon, de kans op prooivangst en de duur van de voedingsperiode worden gerelateerd aan het geschatte voedselniveau in de darm van de predator (paragraaf 3.2).

Dit experiment over het gedrag van de vier predatorspecies werd uitgevoerd op twee substraten: bespinseld blad en onbespinseld blad. Op deze wijze kon de rol van het spinsel bij het fourageergedrag van de roofmijt worden vastgesteld. In het spinsel bleek de ontmoetingssnelheid per eenheid prooidichtheid lager te zijn, omdat zowel roof- als spintmijten zich er langzaam voortbewegen en ook minder tijd aan lopen besteden. Deze trage verplaatsing voorkomt heftige botsingen tussen roof- en spintmijten zodat verstoring van de roofmijt, zoals veelvuldig waargenomen op het onbespinselde substraat, nauwelijks meer optreedt. De coïncidentie tussen predator en prooi en dus ook de ontmoetingssnelheid worden verlaagd door de labyrinthstructuur van het spinsel. Immers predator en prooi kunnen over en onder elkaar doorlopen zonder dat onderling contact plaatsvindt. De predatoren zoeken waarschijnlijk op de tast (paragraaf 3.2.3). Nadat zij een prooi met de zintuigen op de tarsi van het eerste potenpaar hebben ontdekt, kan een aanval worden ingezet. Echter niet elk contact leidt tot een succesvolle prooivangst. De succes ratio bleek af te hangen van de darmvulling van de predator, het ontwikkelingsstadium en het geslacht van de prooi en, in twee bijzondere gevallen, van het substraat; in het spinsel neemt de succes ratio van *Phytoseiulus persimilis* sterk toe, terwijl die van *Amblyseius potentillae* dan juist sterk afneemt (paragraaf 3.2.7, Figuur 33).

Op basis van deze gedragscomponentenanalyse werd een predatiemodel ontworpen met gebruikmaking van wachttijdtheorie (paragraaf 3.3). Deze theorie wordt veel gebruikt bij de analyse van dienstverleningsprocessen, bijvoorbeeld de behandeling van patiënten op het spreekuur van een arts. De patiënten zijn nu de prooien, de arts is de predator, en de wachtkamer is de darm van de predator. De snelheid waarmee zich nieuwe patiënten aanmelden en in de wachtkamer gaan zitten is equivalent met de predatiesnelheid; de tijd die benodigd is voor de behandeling van de patiënt is equivalent aan de tijd die de predator nodig heeft om een prooi te verteren en het verteerde voedsel in de haemolymphe op te nemen. Naarmate er meer patiënten in de wachtkamer zitten, zal de arts de patiënten sneller behandelen en naarmate de wachtkamer voller is, zal er een grotere kans zijn dat de nieuw-aankomende patiënten van een behandeling afzien. Analoog aan dit voorbeeld neemt de snelheid van voedselresorptie toe met toenemende darmvulling, terwijl daarmee de motivatie om nog een prooi te vangen afneemt. Beide tendenzen zijn experimenteel aangetoond.

Aangenomen dat het aantal prooivangsten per tijdseenheid een Poissonverdeling heeft bij een bepaald niveau van de darmvulling en dat de resorptietijd per prooi een negatief exponentiële verdeling heeft, kan een stochastisch wachttijdmodel worden afgeleid. Dit model werd vergeleken met een deterministisch model, een Compound-simulatiemodel en een Monte Carlo-simulatiemodel van het predatieproces (Appendix E-H). Deze vergelijking viel uit in het voordeel van het wachttijdmodel, omdat deze minder rekentijd verbruikt en spaarzaam is in het gebruik van variabelen zonder dat de essenties verloren gaan (paragraaf 3.3.1).

Het wachttijdmodel werd op bruikbaarheid getest in een serie validatie-experimenten, uitgevoerd op bespinselde en onbespinselde substraten (paragraaf 3.3.2 en 3.3.3). Het bleek dat de ontmoetingssnelheid per eenheid prooidichtheid wordt verlaagd door de aanwezigheid van spinsel en dat dit effect resulteert in een verlaagde predatiesnelheid bij *Amblyseius bibens* en *Metaseiulus occidentalis*. Tegenover deze daling in het zoekvermogen staat echter de hoge prooidichtheid die in de spinselaggregaten wordt aangetroffen (20-60 individuen per cm^2 bespinseld blad), zodat de ontmoetingssnelheid tussen predator en prooi toch nog hoog is. De overige twee onderzochte roofmijtenspecies bleken deze effecten ook te ondervinden, maar deze species worden door het bespinselde substraat tevens beinvloed voor wat betreft de kans om een prooi te vangen na tarsaal contact (succes ratio). *Amblyseius potentillae* heeft een lagere succes ratio op het bespinselde blad, hetgeen de verlaging van het zoekvermogen meer dan alleen compenseert: de predatiesnelheid in de prooikolonie is hoger dan op onbespinselde bladeren met dezelfde hoeveelheid prooi.

Systeemanalyse van de predatie bij verschillende temperaturen leerde dat het effect van de temperatuur op de voedselconversiesnelheid bepalend is voor de vraatsnelheid (paragraaf 3.3.4). Gedragsveranderingen ten gevolge van de temperatuur bleken dus van veel minder belang. Vermoedelijk wordt óók de verlaagde reproduktie bij hogere predatordichtheden veroorzaakt door een verlaging van de voedselconversiesnelheid en niet door veranderingen in het zoekgedrag of door tijdverspilling bij onderling contact tussen roofmijten (paragraaf 3.3.6). Omdat roofmijtvrouwtjes streven naar de realisatie van de potentiële eiproduktie is de voedselconversiesnelheid evenals de reproduktiesnelheid niet afhankelijk van de leeftijd maar van het aantal reeds door haar gelegde eieren (paragraaf 3.3.5). Het gebruik van voedsel voor de eiproduktie bleek bij deze predatoren centraal te staan in de bepaling van de predatiesnelheid, terwijl het vermogen om prooien te bemachtigen als een substraat gebonden constante bleek te kunnen worden beschouwd.

Het wachttijdmodel werd tenslotte uitgebreid voor het geval dat meerdere prooistadia met elk een verschillende voedselinhoud aanwezig zijn (paragraaf 3.3.7; Appendix I). De predatie van een bepaald prooistadium wordt in het model bepaald door succes ratios, die gemeten waren in 'monoculturen' van prooistadia. Uit deze metingen bleek dat spinteieren een makkelijker prooi vormen dan larven, larven een makkelijker prooi vormen dan nymphen, en dat de adulte spintvrouwtjes verreweg het moeilijkst te bemachtigen zijn. Bovendien bleek dat de verschillen in prooivangkansen voor de verschillende stadia kleiner worden naarmate de darmvulling van de predator lager is: de predator wordt minder kieskeurig naarmate zij meer honger heeft. Simulatie van de predatie in een 'mengcultuur' suggereerde dat de 'monocultuur' succes ratios ook onder deze omstandigheden de prooivangkans kunnen weergeven. Echter, er moeten nog veel meer validatie-experimenten worden uitgevoerd.

De duur van het verblijf in een prooikolonie wordt vooral bepaald door de prooidichtheid (paragraaf 3.4.1 en 3.4.2). Dit bleek uit de vergelijking van de verblijfsduur van predatoren in spinsels met en zonder prooien. Analyse van het looppatroon en daarop gebaseerde simulaties van de verblijfsduur leerde, dat het kronkelige looppad van de predator geen verklaring kan geven voor de duur van het verblijf in de prooikolonie. De experimenteel vastgestelde verblijfsduur in een prooikolonie kan alleen worden bereikt indien de predator bij de rand van de kolonie omkeert. Volgens de simulaties van het loopgedrag komt de predator vaak genoeg bij de kolonierand om snel te kunnen reageren op verlaging van het prooiaanbod. Doordat roofmijtvrouwtjes blijven zitten in de kolonies met hoge prooidichtheid zal de predatordichtheid ter plekke toenemen. Experimenteel werd aangetoond dat verhoging van de predatordichtheid leidt tot een kortere verblijfsduur ondanks een ruim aanbod van prooien (paragraaf 3.4.3). Predator- en prooidichtheid blijken dus de belangrijkste factoren te zijn die het vertrek van de predator bepalen.

Doordat er onderscheid werd gemaakt tussen gekoloniseerd blad en ongekoloniseerd blad is het niet alleen nodig om de factoren te bepalen die de verblijfsduur in de kolonie regelen, maar ook de factoren die bepalen hoeveel tijd een predator buiten de kolonies doorbrengt, m.a.w. hoe zoekt een roofmijt naar nieuwe prooikolonies? Dit is natuurlijk ook een aspect van het gedrag op het individu-niveau, maar het zal in Deel 2 van dit rapport worden behandeld in samenhang met de kolonisatie van de plant door de spintmijten. Wèl is in Deel 1 reeds besproken (paragraaf 3.4 en 3.3.4) dat de roofmijten langs de bladrand of een nerf lopen en een kolonie binnendringen na tarsaal contact met de spinseldraden. *Amblyseius potentillae* vormt hierop een uitzondering. Deze roofmijt heeft de neiging om de bespinselde bladdelen te mijden en zit bij voorkeur naast de dikke delen van de hoofdnerf of in andere beschermde hoekjes op de plant.

De metingen op het individu-niveau kunnen aanleiding geven tot vragen die slechts door simulatie en experimenten op populatie-niveau kunnen worden opgelost. Denk bijvoorbeeld aan de metingen van het vertrek van de predator uit een prooikolonie bij verschillende prooi- en predatordichtheden. Welke rol speelt dit dispersie-proces in de populatiedynamiek van predator en prooi? Doordat de veranderingen in de aantallen en het kolonisatiepatroon continu plaatsvinden, zou dynamische simulatie in combinatie met populatie-experimenten een oplossing kunnen leveren. Ook het belang van ontbrekende experimentele gegevens op het individu-niveau kunnen worden opgespoord. Denk bijvoorbeeld aan het feit dat de ontwikkelingsduur en de reproduktie zijn gemeten aan individuele spintmijten bij een overmaat aan voedsel. Doordat de spintmijten het bladparenchym leegzuigen zal de kwaliteit van het blad achteruitgaan en mogelijk zullen de groei-variabelen daardoor worden beinvloed. Wanneer dit een rol speelt, dan zouden simulaties van de populatiegroei van de spintmijten een grotere aantalstoename te zien geven dan populatie-experimenten in de kas. Deze voorbeelden laten zien hoe populatiemodellen kunnen worden gebruikt om het belang van bepaalde karakteristieke eigenschappen van prooi of predator voor de populatiedynamiek te demonstreren en om nieuwe metingen op het individu-niveau te rechtvaardigen. Op deze wijze zijn een aantal vragen geformuleerd in Hoofdstuk 4, die opgelost zouden kunnen worden door combinatie van simulatie en experiment op populatieniveau. De beantwoording van deze vragen zal in Deel 2 plaatsvinden.

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APPENDIX A MODEL OF REPRODUCTION IN RELATION TO FOOD INTAKE

```
TITLE REPRODUCTION IN RELATION TO FOOD INTAKE
TITLE DETERMINISTIC SIMULATION OF THE FOOD CONVERSION
TITLE DISCRETE FEEDING SCHEDULE
INITIAL
      DELX=1./DELT
************************************************************************
*** INPUT DATA
*** METASEIULUS OCCIDENTALIS
***
PARAM GUTC=3.3,OPTFW=2.2,DRYW=2.7,EGG=1.9
************************************************************************
*** RELATIVE RATES
***
      RRRES =(TEMP-11.)*0.195
      RREG  =(TEMP-11.)*0.01
      RRWLOS=(TEMP-11.)*0.04
PARAM TEMP  =26.
************************************************************************
*** INITIAL CONDITIONS
***
PARAM FDEPRT=0.
      IFRW  =OPTFW *EXP(-RRWLOS*FDEPRT)
      IFCG  =GUTC  *EXP(-RRRES *FDEPRT)
      IREP  =0.
DYNAMIC
************************************************************************
*** STATE VARIABLES
***
      WEIGHT=FRESHW +DRYW +FCGUT
      FRESHW=INTGRL(IFRW,RRESW-RWLOSS)
      FCGUT =INTGRL(IFCG,RFI-RRES-REG)
      REPROD=INTGRL(IREP,RRESR-PUSH*EGG*DELX)
      NEGG  =INTGRL(0.,PUSH*DELX)
      PUSH  =INSW(REPROD-EGG,0.,1.)
      FOOD  =INTGRL(IFCG,RFI   )
      FAECES=INTGRL(0.   ,REG  )
      MTBOL =INTGRL(0.   ,RRESW)
************************************************************************
*** RATE VARIABLES
***
      RFI   =AMIN1(GUTC-FCGUT,PREY)*PULS*DELX
      RRES  =RRRES *FCGUT
      RRESR =INSW(FRESHW-OPTFW,0.,RRES)
      RRESW =INSW(FRESHW-OPTFW,RRES,0.)
      REG   =RREG  *FCGUT
      RWLOSS=RRWLOS*FRESHW
************************************************************************
*** FEEDING SCHEDULE
***
PARAM PERIOD=1.
      PULS  =IMPULS(0.,PERIOD)
PARAM PREY  =1.
```

```
****************************************************************************
*** OUTPUT STATEMENTS
***
PRINT FOOD,FAECES,MTBOL,FCGUT,FRESHW,WEIGHT,REPROD,NEGG
TIMER FINTIM=50.,OUTDEL=2.,PRDEL=2.,DELT=0.05
METHOD RECT
END
STOP
ENDJOB
```

APPENDIX B TIME SERIES ANALYSIS

Sequential changes of walking directions may be correlated. This can be analysed in two ways:

- Markov chain analysis with regard to the sign of the changes in walking direction;
- Auto correlation analysis with regard to the sign and the magnitude of changes in walking direction.

Markov chain analysis

If a sign of an element in a time series depends on the signs of preceding elements, a Markov model may be adequate. The case most commonly treated is the first order Markov model, for which only the last element in a time series influences the choice of a new element:

$$p_{ji} = \text{Prob}(A_s = i \mid A_{s-1} = j,\ A_{s-2} = k,\ \ldots\ldots) = \text{Prob}(A_s = i \mid A_{s-1} = j)$$

for positive or negative j, i, k .....
This is called a transition probability from j to i. Four transition probabilities are possible: p_{--}, p_{-+}, p_{+-} and p_{++}.

Suppose we want to test the null hypothesis that a direction choice process has order zero (no feedback at all) against the alternative that the order is one (an influence of only the last element). Then it is useful to order the sequences in the following contingency tables:

to from	+	-	total
+	N_{++}	N_{+-}	$N_{+\cdot}$
-	N_{-+}	N_{--}	$N_{-\cdot}$
total	$N_{\cdot+}$	$N_{\cdot-}$	N

For $N_{\cdot+}$*, the point indicates that the first element in a sequence can be either + or -; the second element must be a +. Similarly for* $N_{+\cdot}$ *the first element in a sequence must be a +, the second may be + or -, and so on.*

Under the null hypothesis, $\hat{p}$ equals $N_{\cdot i}/N$ (i = + or -). According to Anderson & Goodman (1957) the following Chi-square statistic applies:

$$\chi_1^2 = \sum_{i=-,+} \left\{ \frac{(N_{i+}-\hat{p}\cdot N_{i\cdot})^2}{\hat{p}\cdot N_{i\cdot}} + \frac{(N_{i-}-(1-\hat{p})\cdot N_{i\cdot})^2}{(1-\hat{p})\cdot N_{i\cdot}} \right\}$$

If this zero-order test reveals dependency, it may be asked if the process is of order one or higher. The null hypothesis of order = 1 can be tested against the alternative of order = 2 with the aid of the following contingency tables:

from \ to	+	-
-+	N_{-++}	N_{-+-}
++	N_{+++}	N_{++-}

from \ to	+	-
--	N_{--+}	N_{---}
+-	N_{+-+}	N_{+--}

According to Anderson & Goodman, these tables may be treated as contingency tables again. The sum of the χ_1^2 statistics has the χ_2^2 distribution under the null hypothesis.

Auto correlation analysis

Correlation between successive observations in a series is called auto correlation (see e.g. Chattfield, 1975). The auto correlation coefficient is calculated with the aid of the covariance coefficient c_k, which by analogy with the ususal covariance formula is defined as:

$$c_k = \frac{1}{n} \sum_{s-1}^{n-k} (A_s - \bar{A}) \cdot (A_{s+k} - \bar{A}).$$

This is called the auto covariance at lag k, in which s is the number of the element in the series. The auto correlation coefficient ρ_k is estimated as the quotient of c_k and the variance σ_A^2 $(=c_{k=0})$:

$$r_k = \frac{c_k}{c_0}\ , \text{ for } k = 1,\ 2,\ \ldots\ldots,\ m \text{ and } m << n.$$

Suppose that A_1, A_2, ...A_n are independent and identically distributed random variables with an arbitrary mean, then it can be shown (Kendall & Stuart, 1966, chapter 48) that:

$$E(r_k) \cong -1/n \qquad \text{and} \qquad \mathrm{var}(r_k) \cong 1/n,$$

and that r_k is asymptotically normally distributed. After plotting of the r_k values against k, approximate 95% confidence limits can be drawn at $-1/n \pm 1/\sqrt{n} \cdot t_{n(\alpha\,=\,0.05)} = -1/n \pm 2/\sqrt{n}$. Values of r_k that fall outside these limits are significantly different from zero at the 5% level.

For the purpose of simulation a multiple regression model is adequate to account for correlation between successive ranges in walking direction A_s $(1 \leqslant s \leqslant n)$. This process can be described by the auto regression equation:

$$A_s = \alpha_1 \cdot A_{s-1} + \alpha_2 \cdot A_{s-2} + \ldots\ldots + \alpha_m \cdot A_{s-m} + X_s, \text{ where } E(X_s) = E(A_s) = 0.$$

A_s is not regressed on independent variables but on past values of A_s. Hence the term auto regression; m is the so-called *order of the auto regressive process*. The coefficients $\alpha_1, \alpha_2, \ldots, \alpha_m$ are the auto regression or partial auto correlation coefficients and X_s is determined by a purely random process. To obtain a series X_s, which is freed of correlation, the auto regression equation is rewritten as

$$X_s = A_s - (\alpha_1 \cdot A_{s-1} + \alpha_2 \cdot A_{s-2} + \ldots\ldots + \alpha_m \cdot A_{s-m}).$$

The parameters μ, σ, and λ of the Tukey distribution may be estimated again on this corrected series X_s.

Now two related questions remain to be answered:

- How to determine the order m of the process?
- How can we estimate the auto regression coefficients from the auto correlations?

The order of the process is indicated by the range of values of r_k or α_k, which are significantly different from zero (i.e. outside the range $\pm 2/\sqrt{n}$).

The relation between α and r can be obtained by multiplying the auto regression equation with A_{s-k} and by calculating expectations:

$$\frac{1}{n-k} \cdot \sum_{s=1}^{n-k} (A_s \cdot A_{s-k}) = \frac{\alpha_1}{n-k} \cdot \sum_{s=1}^{n-k} (A_{s-1} \cdot A_{s-k}) + \ldots\ldots + \frac{\alpha_m}{n-k} \cdot \sum_{s=1}^{n-k} (A_{s-m} \cdot A_{s-k})$$

for $E(X_s) = E(A_s) = 0$.

For n >> k, this equation may be simplified with the aid of the formula for the auto covariance coefficient

$$c_k = \alpha_1 \cdot c_{k-1} + \ldots\ldots + \alpha_m \cdot c_{k-m}.$$

If the auto covariance coefficient c_k is divided by the variance $\hat{\sigma}_A^2$ ($=c_0$), we obtain the Yule-Walker equations:

$$r_k = \alpha_1 \cdot r_{k-1} + \ldots\ldots + \alpha_m \cdot r_{k-m}.$$

Because r_k is equal to r_{-k}, the m unknown auto regression coefficients can be solved out of a set of m Yule-Walker equations. In matrix-notation these equations are:

$$\begin{pmatrix} 1 & r_1 & r_2 & \cdots\cdots & r_{m-1} \\ r_1 & 1 & r_1 & \cdots\cdots & r_{m-2} \\ r_2 & r_1 & 1 & \cdots\cdots & r_{m-3} \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ r_{m-1} & r_{m-2} & r_{m-3} & \cdots\cdots & 1 \end{pmatrix} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \alpha_m \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \\ r_3 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ r_m \end{pmatrix}$$

Note, that for a first order auto regressive process, the auto correlation coefficients decrease exponentially with k:

$$r_k = \alpha_1^k.$$

APPENDIX C MAXIMUM LIKELIHOOD ESTIMATION OF THE PARAMETERS OF THE TUKEY DISTRIBUTION

The procedure to estimate the parameters μ, σ and λ of the Tukey distribution consists of a rough estimation of these parameters to obtain starting values, and a subsequent maximization of the likelihood function to optimize the parameter estimates (van Montfort & Otten, 1976).

Starting values

Estimate approximate values of X_p for the 10%, 30%, 70%, 90% points of the measured cumulative frequency distribution. With these estimations, λ_o can be solved from the following equation by Newton-Raphson iteration:

$$\frac{X_{0.7} - X_{0.3}}{X_{0.9} - X_{0.1}} = \frac{(0.7^{\lambda_o} - 0.3^{\lambda_o}) - (0.3^{\lambda_o} - 0.7^{\lambda_o})}{(0.9^{\lambda_o} - 0.1^{\lambda_o}) - (0.1^{\lambda_o} - 0.9^{\lambda_o})} = \frac{0.7^{\lambda_o} - 0.3^{\lambda_o}}{0.9^{\lambda_o} - 0.1^{\lambda_o}}$$

The 50% point of the cumulative frequency distribution, $X_{0.5}$, serves as a starting value for μ_o. The starting value of σ_o can now be obtained from equation:

$$X_{0.9} = \mu_o + \sigma_o \cdot (0.9^{\lambda_o} - 0.1^{\lambda_o})/\lambda_o$$

Iterative optimization procedure

This procedure is based on Newton-Raphson iteration with the Log-Likelihood function:

$$\begin{pmatrix}\lambda\\ \mu\\ \sigma\end{pmatrix}_{K+1} = \begin{pmatrix}\lambda\\ \mu\\ \sigma\end{pmatrix}_{K} + (-L'')^{-1} \cdot L'$$

K = iterative step number

L = $\ln(L^*)$ (the Log-Likelihood function)

L^* = $\prod_{i=1}^{c} p_i^{n_i}$ (the Likelihood function)

i = 1, 2, ..., c

c = number of frequency classes

n_i = frequency in class i

p_i = probability in class i

Σn_i = N

When g_i is defined as the class boundary, the Log-Likelihood function can be computed as follows:

$$L = \sum_{i=1}^{c} n_i \cdot \ln \left\{ f_\lambda^{-1}\left(\frac{g_{i+1}-\mu}{\sigma}\right) - f_\lambda^{-1}\left(\frac{g_i-\mu}{\sigma}\right) \right\}$$

$$Y_p = f_\lambda(p) \qquad \text{and} \quad p = f_\lambda^{-1}(Y_p)$$

To maximize the Log-Likelihood function, L, the first and second derivatives L' and L" are needed. Because of the discrete character of the L function, these derivatives are determined numerically, according to Abramowitz & Stegun (1975, p. 883-884).

$$L' = \begin{pmatrix} \frac{\delta L}{\delta\lambda} \\ \frac{\delta L}{\delta\mu} \\ \frac{\delta L}{\delta\sigma} \end{pmatrix} \; ; \quad L'' = \begin{pmatrix} \frac{\delta L^2}{\delta\lambda\delta\lambda} & \frac{\delta L^2}{\delta\lambda\delta\mu} & \frac{\delta L^2}{\delta\lambda\delta\sigma} \\ \frac{\delta L^2}{\delta\mu\delta\lambda} & \frac{\delta L^2}{\delta\mu\delta\mu} & \frac{\delta L^2}{\delta\mu\delta\sigma} \\ \frac{\delta L^2}{\delta\sigma\delta\lambda} & \frac{\delta L^2}{\delta\sigma\delta\mu} & \frac{\delta L^2}{\delta\sigma\delta\sigma} \end{pmatrix}$$

It is possible that -L" has a negative eigenvalue in the beginning of the iterative procedure. Therefore van Montfort & Otten (1977) propose a reparameterization to reduce this inconvenience. This is done by replacement of σ by $S = \sigma \cdot Y_{p(K=1)}$ for $p(K=1) = \frac{e}{1 + e} = 0.731 \ldots$

The iteration process can be stopped when $L_K - L_{K-1}$ or L' or $\left| \begin{pmatrix} \lambda \\ \mu \\ \sigma \end{pmatrix}_{K+1} - \begin{pmatrix} \lambda \\ \mu \\ \sigma \end{pmatrix}_K \right|$ is sufficiently small. A χ^2_{c-1-3} test (c = number of frequency classes) is used to test the fit of the Tukey model to the measured frequency data. A confidence interval for the parameters can be constructed on the basis of the covariance matrix

$$\text{cov} \begin{pmatrix} \lambda \\ \mu \\ \sigma \end{pmatrix} = \frac{1}{N} \cdot (-L'')^{-1}.$$

APPENDIX D MODEL OF WALKING BEHAVIOUR

```
 TITLE TORTUOUS WALK + PREDATION
/     DIMENSION C(100,100)
FIXED U,I,J,K,X,Y
INITIAL
      DELX  =1./DELT
INCON U     =1
PARAM UNIT  =.5
***********************************************************
*** PROPERTIES OF PREY AND PREDATOR
***
      SPEED =0.018*60.
      DIAM1 =0.091
      DIAM2 =0.013
      RADIUS=0.5*(DIAM1+DIAM2)/UNIT
PARAM LABDA=-0.85,SIGMA=0.2,MU=0.
NOSORT
***
***********************************************************
*** REGULAR DISTRIBUTION OF THE PREY
***
      DO 1 I=1,99
      DO 1 J=1,99
      C(I,J)=1.
 1    CONTINUE
DYNAMIC
***
***********************************************************
*** NON-AUTOCORRELATED WALK
***
      P     =RNDGEN(U)
      A     =MU+SIGMA*(P**LABDA-(1.-P)**LABDA)/LABDA
      DIR   =INTGRL(0.,A*DELX)
      CSDR  =COS(DIR)
      SNDR  =SIN(DIR)
      X1    =INTGRL(50.,CSDR/UNIT)
      Y1    =INTGRL(50.,SNDR/UNIT)
NOSORT
***
**********************************************************
*** REGISTRATION OF PREDATOR-PREY ENCOUNTERS
***
      DO 3 I=1,7
      DO 3 J=1,7
      X     =X1-4+I
      Y     =Y1-4+J
      IF (C(X,Y).EQ.0.) GO TO 3
      DIST  =SQRT((X-X1)**2+(Y-Y1)**2)
      IF (DIST.GT.RADIUS) GO TO 3
      WRITE(6,100) X,Y
 100  FORMAT(1X,2(F3.0,1X))
      C(X,Y)=0.
      SUM   =SUM+1.
 3    CONTINUE
SORT
      CLOCK =TIME/SPEED
***
```

```
********************************************************
*** OUTPUT STATEMENTS
***
PRINT SUM,CLOCK
TIMER FINTIM=100.,PRDEL=1.,OUTDEL=0.04,DELT=0.04
METHOD RECT
FINISH X1=0.5,X1=99.5,Y1=0.5,Y1=99.5
INTERACTIVE
OUTPUT X1(30.,70.),Y1(30.,70.)
 LABEL PHYTOSEIULUS PERSIMILIS
  PAGE XYPLOT
END
STOP
ENDJOB
```

APPENDIX E DETERMINISTIC MODEL OF THE PREDATION PROCESS

```
TITLE FUNCTIONAL RESPONSE OF A PREDATOR TO THE DENSITY OF ITS PREY
TITLE DETERMINISTIC APPROACH
TITLE YOUNG FEMALE PREDATOR OF METASEIULUS OCCIDENTALIS VERSUS
TITLE EGGS OF TETRANYCHUS URTICAE

**********************************************************************
***  PHYSIOLOGICAL AND BEHAVIOURAL INPUT VARIABLES
***
PARAM GUTCON=3.3
PARAM FCPREY=1.
INCON IFCG  =2.95
PARAM TEMP  =26.
      RRGE  =(TEMP - 11.) * 0.195
PARAM DMPREY=0.013
PARAM DMPRED=0.057
      DM    =DMPREY + DMPRED
PARAM VLPREY=0.
PARAM ACPREY=0.
PARAM COIN  =0.42
      VLPRED=AFGEN(VLPT,FCG/GUTCON)
      ACPRED=AFGEN(ACPT,FCG/GUTCON)
      SR    =AFGEN(SRT ,FCG/GUTCON)
      FT    =AFGEN(FTT ,FCG/GUTCON)
FUNCTION VLPT=0.,0.047,1.,0.047
FUNCTION ACPT=0.,0.39,1.,0.39
FUNCTION FTT =0.,.009,.1,.007,.2,.006,.3,.005,.4,.004,1.,.004
FUNCTION SRT =0.,.558,.05,.936,.1,.854,.2,.273,.3,.217,.4,.152, ...
              .5,.083,.6,.103,.7,.0469,.8,.0217,.9,.007,.98,0.,1.1,0.
***
************************************************************************
***  COMPUTATION OF THE RATE OF SUCCESSFUL ENCOUNTER
***
      RREWW =DM *SQRT(VLPREY**2 + VLPRED**2)*ACPREY*ACPRED
      RREWR =DM * VLPRED * ACPRED * (1. - ACPREY)
      RRERW =DM * VLPREY * ACPREY * (1. - ACPRED)
      RSA   =(RREWW + RREWR + RRERW) * DPREY * COIN * SR * 86400.
      TSC   =FT + (1./AMAX1(RSA,1.E-5))
      RSE   =1./TSC
      CUMPRD=INTGRL(0.,RSE)
***
************************************************************************
*** DYNAMICS OF THE FOOD CONTENT OF THE GUT
***
      FCG   =INTGRL(IFCG, RFI - RGE )
      RGE   =RRGE * FCG
      RFI   =AMIN1(SDG/DELT,RSE *FCPREY)
      SDG   =AMAX1(0.,GUTCON - FCG)
***
************************************************************************
***  FLUCTUATION OF THE PREY DENSITY IN RELATION TO
***  THE TIME INTERVAL OF PREY REPLACEMENT
***
```

```
      DPREY =INTGRL(IDPREY,(-RSE/AREA) + (REPL * (IDPREY-DPREY)/DELT))
PARAM NPREY=125.
PARAM AREA  =5.
      IDPREY=NPREY/AREA
      REPL  =IMPULS(0.,REPDEL)
      REPDEL=0.5/24.

***
*************************************************************************
*** OUTPUT STATEMENTS
***
PRINT CUMPRD, FCG , DPREY
TIMER FINTIM=0.25,PRDEL=0.01,DELT=0.001
METHOD RECT
***
*************************************************************************
END
STOP
ENDJOB
```

APPENDIX F MONTE CARLO SIMULATION OF THE PREDATION PROCESS

```
TITLE FUNCTIONAL RESPONSE OF A PREDATOR TO THE DENSITY OF ITS PREY
TITLE MONTE CARLO APPROACH
TITLE YOUNG FEMALE PREDATOR OF METASEIULUS OCCIDENTALIS VERSUS
TITLE EGGS OF TETRANYCHUS URTICAE

***********************************************************************
***  PHYSIOLOGICAL AND BEHAVIOURAL INPUT VARIABLES
***
PARAM GUTCON=3.3
PARAM IFCP  =1.
INCON IFCG  =2.95
PARAM TEMP  =26.
      RRFI  =1.8*60.*24.
      RRGE  =(TEMP - 11.) * 0.195
PARAM DMPREY=0.013
PARAM DMPRED=0.057
      DM    =DMPREY + DMPRED
PARAM VLPREY=0.
PARAM ACPREY=0.
PARAM COIN  =0.42
      VLPRED=AFGEN(VLPT,FCG/GUTCON)
      ACPRED=AFGEN(ACPT,FCG/GUTCON)
      SR    =AFGEN(SRT ,FCG/GUTCON)
      FT    =AFGEN(FTT ,FCG/GUTCON)
FUNCTION VLPT=0.,0.047,1.,0.047
FUNCTION ACPT=0.,0.39,1.,0.39
FUNCTION FTT =0.,.009,.1,.007,.2,.006,.3,.005,.4,.004,1.,.004
FUNCTION SRT =0.,.558,.05,.936,.1,.854,.2,.273,.3,.217,.4,.152, ...
              .5,.083,.6,.103,.7,.0469,.8,.0217,.9,.007,.98,0.,1.1,0.
***
*******************************************************************
***  ENGAGEMENT OF THE PREDATOR
***
FIXED HANDLE
      HANDLE= 0.5 + INTGRL(0.,(CATCH-ABAND)/DELT)
      SEARCH=1. - HANDLE
      HTIM  =INTGRL(0.,RHTIM)
      RHTIM = FT*CATCH/DELT - INSW(DELT-HTIM,1.,HTIM/DELT)
      ABAND =INSW(-HTIM,0.,1.) * HANDLE
***
*************************************************************************
***  COMPUTATION OF THE RATE OF SUCCESSFUL ENCOUNTER
***
      RREWW =DM *SQRT(VLPREY**2 + VLPRED**2)*ACPREY*ACPRED
      RREWR =DM * VLPRED * ACPRED * (1. - ACPREY)
      RRERW =DM * VLPREY * ACPREY * (1. - ACPRED)
      RSE   =(RREWW + RREWR + RRERW) * DPREY * COIN * SR * 86400.
      PRC   =1. - EXP(-RSE*DELT)
      RDRAW =RNDGEN(TELLER*200.)
      CATCH =INSW(PRC - RDRAW , 0. , 1. ) * SEARCH
      CUMPRD=INTGRL(0.,CATCH*INTERV/DELT)
      INTERV=INSW(TIME-ADAPT,0.,1.)
PARAM ADAPT =0.1
***
```

```
**********************************************************************
*** DYNAMICS OF THE FOOD CONTENT OF THE GUT
***
      FCG   =INTGRL(IFCG, RFI - RGE )
      RGE   =RRGE * FCG
      RFI   =AMIN1(SDG,FCPREY)*HANDLE*RRFI
      SDG   =AMAX1(0.,GUTCON - FCG)
      FCPREY=INTGRL(0.,CATCH*(IFCP-FCPREY)/DELT - RFI )
      AFCG  =INTGRL(0.,FCG/DELT/NUM*IMPULS(ADAPT,PERIOD))
      NUM   =(FINTIM-ADAPT)/PERIOD
PARAM PERIOD=0.05
***
**********************************************************************
***   FLUCTUATION OF THE PREY DENSITY IN RELATION TO
***   THE TIME INTERVAL OF PREY REPLACEMENT
***
      DPREY =INTGRL(IDPREY,((-CATCH/AREA)+REPL*(IDPREY-DPREY))/DELT)
PARAM NPREY =125.
PARAM AREA  =5.
      IDPREY=NPREY/AREA
      REPL  =IMPULS(0.,REPDEL)
      REPDEL=0.5/24.
***
**********************************************************************
*** OUTPUT STATEMENTS
***
TIMER FINTIM=0.25,PRDEL=0.01,DELT=0.001
METHOD RECT
TERMINAL
PARAM NREP  =100.
INCON MPRED=0.,MFCG=0.
INCON SPRED=0.,SFCG=0.
INCON VPRED=0.,VFCG=0.
INCON TELLER=0.
      MPRED =MPRED+CUMPRD/NREP
      MFCG  =MFCG + AFCG /NREP
      SPRED =SPRED+CUMPRD*CUMPRD
      SFCG  =SFCG + AFCG * AFCG
      TELLER=TELLER+1.
      IF (TELLER.GE.NREP) GO TO 1
      CALL RERUN
      GO TO 2
 1    VPRED =(SPRED-NREP*MPRED*MPRED)/(NREP-1.)
      VFCG  =(SFCG -NREP*MFCG*MFCG)/(NREP-1.)
      WRITE(6,100) IDPREY
 100  FORMAT(11H DENSITY = ,F8.0)
      WRITE(6,101) REPDEL
 101  FORMAT(23H REPLACEMENT IN DAYS = ,F8.4)
      WRITE(6,102)
 102  FORMAT(25H MPRED, VPRED, MFCG, VFCG)
      WRITE(6,103) MPRED,VPRED,MFCG,VFCG
 103  FORMAT(2(4X,2(F8.4,4X)))
 2    CONTINUE
***
**********************************************************************
END
STOP
ENDJOB
```

APPENDIX G MATRIX ALGEBRAIC SOLUTION OF THE QUEUEING EQUATIONS

Under conditions of constant RSE_n and $\mathrm{RGE1}_n$ the queueing equations can be solved as follows:

Let A be the matrix of the coefficients in the queueing equations

$$A = \begin{pmatrix} 1-\mathrm{RSE}_0 & \mathrm{RGE1}_1 & 0 & 0 \cdots\cdots & 0 & 0 & 0 \\ \mathrm{RSE}_0 & 1-\mathrm{RSE}_1-\mathrm{RGE1}_1 & \mathrm{RGE1}_2 & 0 \cdots\cdots & 0 & 0 & 0 \\ 0 & \mathrm{RSE}_1 & 1-\mathrm{RSE}_2-\mathrm{RGE1}_2 & \mathrm{RGE1}_3 \cdots\cdots & 0 & 0 & 0 \\ 0 & 0 & \mathrm{RSE}_2 & & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & & \mathrm{RGE1}_{N-1} & 0 \\ \cdot & \cdot & \cdot & & \mathrm{RSE}_{N-1} & 1-\mathrm{RSE}_{N-1}-\mathrm{RGE}_{N-1} & \mathrm{RGE1}_N \\ 0 & 0 & 0 \cdots\cdots & \cdots\cdots & 0 & \mathrm{RSE}_{N-1} & 1-\mathrm{RGE1}_N \end{pmatrix}$$

Let p be a vector of the state probabilities, p_n, in the queueing equations

$$p(t) = \begin{pmatrix} p_0(t) \\ p_1(t) \\ p_2(t) \\ \cdot \\ \cdot \\ p_N(t) \end{pmatrix}$$

When R stand for a square matrix of eigenvectors arranged in columns, then a matrix Q can be obtained with the eigenvalues of A (= q_n) ranked on its diagonal

$$Q = R^{-1} \cdot A \cdot R = \begin{pmatrix} q_0 & 0 \cdots\cdots & 0 \\ 0 & q_1 \cdots\cdots & 0 \\ \cdot & \cdot \quad \cdot & \cdot \\ \cdot & \cdot \qquad \cdot & \cdot \\ \cdot & \cdot \qquad\quad \cdot & \cdot \\ 0 & 0 \cdots\cdots & q_N \end{pmatrix}$$

The distribution of $p_n(t)$ can now be calculated as follows

$$p(t) = e^{A\cdot t}\cdot p(0) = R\cdot(e^{R^{-1}\cdot A\cdot R})\cdot R^{-1}\cdot p(0) = R\cdot e^{Q\cdot t}\cdot R^{-1}\cdot p(0)$$

$$e^{Q\cdot t} = \begin{pmatrix} e^{q_0\cdot t} & \cdots\cdots\cdots & 0 \\ . & . & . \\ . & . & . \\ . & . & . \\ . & . & . \\ 0 & \cdots\cdots\cdots & e^{q_N\cdot t} \end{pmatrix}$$

The solution of this set of equations is represented by β_{nn}

$$p_n(t) = \beta_{n0} + \sum_{j=1}^{N} \beta_{nj}\cdot e^{q_j\cdot t}$$

$n = 1, 2, 3, \ldots\ldots. N$

q is negative

β_0 = equilibrium coefficients

The number of prey killed during a time span t (= $CUMPRD_t$) can be found by integration of the predation equation

$$PRED_t' = \lim_{DELT\to 0} PRED = \frac{dPRED_t}{dt} = \sum_{n=0}^{N} n\cdot p_n'(t) + \sum_{n=0}^{N} RGE1_n\cdot p_n(t)$$

$$CUMPRD_t = \sum_{n=0}^{N} n\cdot p_n(t) + \sum_{n=0}^{N} (RGE1_n\cdot \int_0^t p_n(u)du)$$

$$\int_0^t p_n(u)du = \beta_{n0}\cdot t + \frac{1}{q_1}\cdot\beta_{n1}\cdot(1-e^{-q_1\cdot t}) + \frac{1}{q_2}\cdot\beta_{n2}\cdot(1-e^{-q_2\cdot t}) + \ldots$$

```
TITLE FUNCTIONAL RESPONSE OF A PREDATOR TO THE DENSITY OF ITS PREY
TITLE QUEUEING APPROACH
TITLE YOUNG FEMALE PREDATOR OF METASEIULUS OCCIDENTALIS VERSUS
TITLE EGGS OF TETRANYCHUS URTICAE
STORAGE PST(22),PTD(22)
FIXED NCL
INITIAL
**********************************************************************
***  ENUMERATION OF THE FOOD CONTENT CLASSES OF THE GUT
***    1  2  3  4  5 ...... I ......19 20 21 22     = NC
***       1  2  3  4 ...... N ......18 19 20        = NCL
***       0  1  2  3 ...............17 18 19       = NCLASS
***
      NC =22
      NL =NC-1
      NCL=20
      NCLASS =19
***
**********************************************************************
***  COMPUTATION OF THE FLUCTUATION OF PREY DENSITY IN RELATION TO
***  THE TIME INTERVAL OF PREY REPLACEMENT
***
PARAM AREA  =5.
PARAM NPREY =(.1,.25,1.,2.,3.,4.,6.,8.,12.,32.,50.,75.,100.,125.,200.)
      IDPREY=NPREY/AREA
      DPREY =IDPREY
      DELX  =1./DELT
      REPDEL=0.5/24.
PARAM TEMP  =26.
      RRGE  =(TEMP-11.)*0.195
      MDPREY=0.
      MFCG =0.
      CUMPRD=0.
DYNAMIC
      REPL  =IMPULS(0.,REPDEL)
NOSORT
      CALL PREDA(RRGE,DPREY,PRED,FOOD,FCG)
      DPREY =DPREY -(PRED /AREA)+REPL*(IDPREY -DPREY )
      IF (TIME.LT.DELT) GO TO 5
      CUMPRD=CUMPRD+ PRED
      MDPREY=MDPREY+(DPREY*DELT/FINTIM)
      MFCG  =MFCG  +(FCG  *DELT/FINTIM)
***
**********************************************************************
***  OUTPUT STATEMENTS
***
      IF (TIME.LT.FINTIM) GO TO 5
      WRITE(6,111) CUMPRD ,MDPREY ,MFCG
 111  FORMAT(2X,3(2X,F6.3,2X))
*      DO 5 IG=1,NCL
*      GUTCON =IG
*      WRITE(6,112) GUTCON,PST(IG+1),PTD(IG+1)
* 112  FORMAT(2X,3(2X,F8.4,2X))
 5    CONTINUE
```

```
SORT
TIMER FINTIM=.25,PRDEL=.25,DELT=.001
***
************************************************************************
END
STOP
      SUBROUTINE PREDA(RRGEMP,DS,
     $                 PN,FI,GT)
COMMON
C*********************************************************************
C**  PHYSIOLOGICAL AND BEHAVIOURAL INPUT DATA
C**
      DIMENSION RSE(22),RS1(22)
      DIMENSION SR(20) ,FT(20)
      DIMENSION PT(22) ,RGE1(22)
      DIMENSION VL(20) ,AC(20)
      DATA VL/20*.047/
      DATA AC/20*.39/
      DATA SR/.936,.936,.854,.273,.245,.217,.185,.152,.128,.103,
     $        .093,.083,.065,.047,.034,.0217,.014,.007,.0035,0./
      DATA FT/2*.009,2*.007,2*.006,4*.005,10*.004/
      FCP   =1.
      GUTC  =3.333
      ENLARG=NCLASS/GUTC
      DMPREY=0.013
      DMPRED=0.057
      DM    =DMPRED+DMPREY
      VLPREY=0.
      ACPREY=0.
      COIN  =0.42
C***
C***********************************************************************
C***  COMPUTATION OF THE RATE OF SUCCESSFUL ENCOUNTER AND
C***  THE INVERSE OF THE TIME NEEDED TO RESORB AND EGEST
C***  THE MASS EQUIVALENT TO THE CLASS-SPECIFIC PART OF THE PREY
C***
      DO 51 N=1,NCL
      I=N+1
      RGE1(I)=-RRGEMP/ALOG((N-.99)/N)
      RREWW  =DM*SQRT(VL(N)*VL(N)+VLPREY*VLPREY)*AC(N)*ACPREY
      RREWR  =DM*VL(N)*AC(N)*(1.-ACPREY)
      RRERW  =DM*VLPREY*ACPREY*(1.-AC(N))*0.5
      RSA    =(RREWW+RREWR+RRERW)*DS*SR(N)*COIN*86400.
      TSC    =(FT(N))+(1./(AMAX1(RSA,1.E-5)))
      RSE(I) =1./TSC
      PST(I) =0.
 51   CONTINUE
      RGE1(1 )=0.
      RGE1(NC)=1.
      RGE1(2 )=0.
      RSE(1) =0.
      RSE(NL)=0.
      RSE(NC)=0.
C***
C***********************************************************************
C***  COMPUTATION OF THE STEADY STATE DISTRIBUTION OF
C***  THE FOOD CONTENT OF THE GUT
C***
      PST(1) =0.
      PST(NC)=0.
      PST(2) =1.
      SUMST  =0.
      DO 52 N=1,NCL
      I=N+1
      FCPREY =AMIN1(NL-2.,FCP*ENLARG)
```

```
      I1      = MAX1(I-FCPREY,1.)
      PST(I+1)=(-PST(I1)*RSE(I1)+PST(I)*(RSE(I)+RGE1(I)))/RGE1(I+1)
      SUMST   =SUMST+PST(I)
 52   CONTINUE
      DO 53 N=1,NCL
      I=N+1
      PST(I) =PST(I)/SUMST
 53   CONTINUE
C***
C***********************************************************************
C***  INITIALIZATION OF THE FREQUENCY DISTRIBUTION OF
C***  FOOD CONTENT OF THE GUT
C***
      PT(1 ) =0.
      PT(NC) =0.
      DO 54 N=1,NCL
      I=N+1
      PT(I)  =PTD(I)
      IF (TIME.LE.DELT) PT(I) = PST(I)
      RS1(I) =0.
 54   CONTINUE
C***
C***********************************************************************
C***  COMPUTATION OF THE RATE OF PREDATION AND THE FOOD INTAKE
C***  ACCOUNTING FOR PARTIAL INGESTION
C***
      PN =0.
      FI =0.
      IP =FCP*ENLARG
      I1 =MAX0(NCL-IP+1,2)
      DO 55 N=I1,NCL
      I=N+1
      PART   =RSE(I)*PT(I)*DELT
      RS1(NL)=RS1(NL)+PART/DELT
      PN     =PN+PART
      FI     =FI+PART*(NL-I)
 55   CONTINUE
      I2 =MIN0(NCL,IP)
      DO 56 N=I2,NCL
      I=N+1
      WHOLE =RSE(I-IP)*PT(I-IP)*DELT
      RS1(I)=RS1(I)+WHOLE/DELT
      PN     =PN+WHOLE
      FI     =FI+WHOLE*IP
 56   CONTINUE
C***
C***********************************************************************
C***  COMPUTATION OF THE FREQUENCY DISTRIBUTION OF FCGUT
C***  AT TIME + DELT
C***
      SUM    =0.
      DO 57 N=1,NCL
      I=N+1
      RS1(I) =(RS1(I) +RGE1(I+1)*PT(I+1))*DELT
      PTD(I) = PT(I)*(1.-(RSE(I)+RGE1(I))*DELT)+RS1(I)
      SUM    =SUM + PTD(I)
 57   CONTINUE
      GT     =0.
      GUT    =0.
      DO 58 N=1,NCL
      I=N+1
      PTD(I) =PTD(I) /SUM
      G      =N-.5
      GUT    =GUT+PTD(I) *G/ENLARG
      GT     =GT +PST(I) *G/ENLARG
```

```
 58   CONTINUE
C***
C************************************************************************
      RETURN
      END
ENDJOB
```

```
TITLE FUNCTIONAL RESPONSE OF A PREDATOR TO
TITLE THE DENSITY OF A MIXTURE OF PREY STAGES
TITLE QUEUEING APPROACH
TITLE YOUNG FEMALE PREDATOR OF METASEIULUS OCCIDENTALIS VERSUS
TITLE ALL PREY STAGES OF TETRANYCHUS URTICAE
TITLE EGG,LARVA,PROTO- AND DEUTONYMPH C.Q. CHRYSALES,MALE AND FEMALE
STORAGE DSI(10),DS(10),PST(22),PTD(22),PN(10)
FIXED NCL,NST
INITIAL
      NCL=20
      NST=9
***
**********************************************************************
*** COMPUTATION OF THE FLUCTUATION OF THE DENSITIES OF SEVERAL
*** PREY STAGES IN RELATION TO THE TIME INTERVAL OF PREY REPLACEMENT
***
INCON RP=0.,WP=0.,SP=0.
NOSORT
      DO 1 IS=1,NST+1
      DSI(IS)=0.
      DS(IS) =0.
      PN(IS) =0.
 1    CONTINUE
PARAM AREA   =5.
PARAM NPREY  =(0.,2.,5.,8.,10.)
      DSI(2) =NPREY/AREA
      DSI(9) =(10.-NPREY)/AREA
      DO 2 IG=1,NCL+2
      PTD(IG)=0.
 2    CONTINUE
SORT
      DELX  =1./DELT
      REPDEL=12./24.
PARAM TEMP  =25.
      RRGE  =(TEMP-11.)*0.16
DYNAMIC
      REPL  =IMPULS(0.,REPDEL)
NOSORT
      CALL PRED(RRGE,RP,WP,FCG)
      DO 4 IS=2,9,7
      DS(IS) =DS(IS)-(PN(IS)/AREA)+REPL*(DSI(IS)-DS(IS))
      PN(IS) =PN(IS)*DELX
***
**********************************************************************
*** OUTPUT STATEMENTS
***
      IF (TIME.LT.DELT) GO TO 4
      WRITE(6,111) PN(IS),DS(IS),FCG
 111  FORMAT(2X,3(2X,F8.4,2X))
 4    CONTINUE
      PERC=PN(9)/(PN(2)+NOT(PN(2)))
      WRITE(6,110) PERC
 110  FORMAT(2X,1(2X,F8.4,2X))
*      DO 5 IG=1,NCL
*      GUTCON =IG
```

```
*      IF (TIME.LT.DELT) GO TO 5
*      WRITE(6,112) GUTCON,PST(IG+1),PTD(IG+1)
* 112  FORMAT(2X,3(2X,F8.4,2X))
* 5    CONTINUE
SORT
TIMER FINTIM=.001,PRDEL=.001,DELT=.001
END
PARAM AREA=50.
END
PARAM AREA=500.
END
STOP
      SUBROUTINE PRED(RRGEMP,
     $                REPR,WEIGHT,GUT)
COMMON
C**********************************************************************
C*** PHYSIOLOGICAL AND BEHAVIOURAL INPUT DATA
C***
      DIMENSION PT(22),RGE1(22)
      DIMENSION RS(22,10),RS1(22)
      DIMENSION PY(9),SR(20,9),FT(10,9)
      DIMENSION DM(10),VP(20),VL(10),AC(10)
      DATA PY/1.,1.3,1.1,2.3,2.5,2.7,8.6,2.7,18./
      DATA DM/.013,2*.026,3*.034,.045,.084,.065,0.076/
      DATA VL/0.,.004,0.,.007,0.,.01,.01,.02,.02,.068/
      DATA VP/5*0.085,5*0.08,5*0.075,5*0.068/
      DATA AC/0.,.04,0.,.04,0.,.04,.04,.04,.04,.14/
      DATA SR/20*0.,
     $         .774,.908,.883,.884,.880,.880,.861,.861,.728,.728,
     $         .741,.741,.679,.679,.541,.541,.452,.307,.110,0.,
     $           20*0.,
     $           20*0.,
     $           20*0.,
     $           20*0.,
     $           20*0.,
     $           20*0.,
     $           .325,.325,.302,.115,.115,.08,.08,.07,.07,.06,
     $           .06,.06,.06,.06,.06,.05,.05,.04,.02,0./
      DATA FT/10*0.,
     $         8.6,6.3,6.3,5.4,5.8,5.3,5.1,6.0,4.3,2.5,
     $         .011,.011,.009,.008,.007,.006,.005,.005,.005,.005,
     $         .015,.013,.011,.011,.010,.010,.009,.008,.008,.008,
     $         .015,.013,.011,.011,.010,.010,.009,.008,.008,.008,
     $         .015,.013,.011,.011,.010,.010,.009,.008,.008,.008,
     $         .024,.021,.020,.020,.019,.014,.010,.009,.009,.009,
     $         .027,.023,.023,.023,.023,.022,.020,.020,.018,.015,
     $         .040,.032,.031,.027,.026,.021,.021,.019,.019,.019/
      NL=NCL+1
      NC=NCL+2
      MP=NST+1
      GUTC   =5.2
      ENLARG =(NCL-1.)/GUTC
      GUTM   =21.
      OPTW   =4.5
      EGG    =3.2
      DLT    =DELT
      DO 50 M=1,NST
      PN(M)  =0.
      RS(1,M)=0.
      RS(NC,M)=0.
 50   CONTINUE
      DO 51 N=1,NCL
      I=N+1
      PST(I)  =0.
      RS(I,MP)=0.
 51   CONTINUE
C***
```

```
C*********************************************************************
C*** COMPUTATION OF THE RATE OF SUCCESSFUL ENCOUNTER AND
C*** THE INVERSE OF THE TIME NEEDED TO RESORB AND EGEST
C*** THE MASS EQUIVALENT TO THE CLASS-SPECIFIC PART OF THE PREY
C***
      DO 52 N=1,NCL
      I=N+1
      RGE1(I)=-RRGEMP/ALOG((N-.99)/N)
      DO 52 M=1,NST
      AC2    =0.013*(TEMP-11.9)*AC(M)/0.1094
      AC1    =AC(MP)
      ENCAA  =(DM(MP)+DM(M))*SQRT(VP(N)*VP(N)+VL(M)*VL(M))*AC1*AC2
      ENCAR  =(DM(MP)+DM(M))*VP(N)*AC1*(1.-AC2)
      ENCRA  =(DM(MP)+DM(M))*VL(M)*AC2*(1.-AC1)*0.33
      RSE    =(ENCAA+ENCAR+ENCRA)*DS(M)*SR(N,M)*86400.
      TSC    =(FT(I/2,M)/86400.)+(1./(AMAX1(RSE,1.E-5)))
      RS(I,M)=1./TSC
      RS(NL,M)=0.
      RS(I,MP)=RS(I,MP)+RS(I,M)
 52   CONTINUE
      RGE1(1 )=0.
      RGE1(NC)=1.
      RGE1(2) =0.
C***
C*********************************************************************
C*** COMPUTATION OF THE STEADY STATE DISTRIBUTION OF
C*** THE FOOD CONTENTS OF THE GUT
C***
      SUMST  =0.
      PST(1) =0.
      PST(2) =1.
      DO 54 N=1,NCL
      I=N+1
      RS1(I) =0.
      DO 53 M=1,NST
      PREY   =AMIN1(GUTM-2.,PY(M)*ENLARG)
      I1     = MAX1(I-PREY,1.)
      RS(1,M)=0.
      RS1(I) =RS1(I)+PST(I1)*RS(I1,M)
      RS(NL,M)=0.
 53   CONTINUE
      RGE1(2) =0.
      PST(I+1)=(-RS1(I)+PST(I)*(RS(I,MP)+RGE1(I)))/RGE1(I+1)
      SUMST   =SUMST+PST(I)
 54   CONTINUE
      DO 55 N=1,NCL
      I=N+1
      PST(I) =PST(I)/SUMST
 55   CONTINUE
C***
C*********************************************************************
C*** INITIALIZATION OF THE FREQUENCY DISTRIBUTION OF
C*** FOOD CONTENTS OF THE GUT
C***
      PT(1 ) =0.
      PT(NC) =0.
      DO 56 N=1,NCL
      I=N+1
      PT(I)  =PTD(I)
      IF (TIME.LE.DLT) PT(I) = PST(I)
      RS1(I) =0.
 56   CONTINUE
C***
C*********************************************************************
C*** COMPUTATION OF THE RATE OF PREDATION
C***
```

```
      DO 58 N=1,NCL
      I=N+1
      DO 58 M=1,NST
      PREY    =AMIN1(GUTM-2.,PY(M)*ENLARG)
      I2      = MIN1(GUTM-PREY+N,GUTM)
      I1      = MAX1(I   -PREY  ,1. )
      WHOLE   =RS(I1,M)*PT(I1)*DLT
      PART    =RS(I2,M)*PT(I2)*DLT
      RS1(I)  =RS1(I)  +WHOLE/DLT
      RS1(NL)=RS1(NL)+PART /DLT
      PN(M)   =PN(M)   +PART+WHOLE
 58   CONTINUE
C***
C***********************************************************************
C*** COMPUTATION OF THE FREQUENCY DISTRIBUTION OF FCGUT
C*** AT TIME + DELT
C***
      RGE     =0.
      SUM     =0.
      DO 59 N=1,NCL
      I=N+1
      DIG     =RGE1(I+1)*PT(I+1)
      RGE     =RGE+DIG/ENLARG
      RGE1(2)=0.
      PTD(I)  =PT(I)*(1.-(RS(I,MP)+RGE1(I))*DLT)+(RS1(I)+DIG)*DLT
      SUM     =SUM   +PTD(I)
 59   CONTINUE
      GT      =0.
      GUT     =0.
      DO 60 N=1,NCL
      I=N+1
      PTD(I)  =PTD(I)/SUM
      G       =N-.5
      GUT     =GUT+PTD(I)*G/ENLARG
      GT      =GT +PST(I)*G/ENLARG
 60   CONTINUE
C***
C***********************************************************************
C*** REPRODUCTION IN RELATION TO FOOD INTAKE
C***
      IF (TIME.EQ.DLT) FRESHW=OPTW
      WEIGHT  =AMIN1(OPTW,FRESHW)
      FRESHW  =FRESHW+(RGE-(TEMP-11.)*(GUT*0.01+WEIGHT*0.04))*DLT
      PROD    =AMAX1(0.,FRESHW-OPTW)
      FRESHW  =FRESHW-PROD
      REPR    =REPR+(PROD/EGG)
C***
C***********************************************************************
      RETURN
      END
ENDJOB
```

APPENDIX J LIST OF ABBREVIATIONS USED IN COMPUTER PROGRAMS

A = angular deviation
ABAND = abandoning the captured prey
AC- = activity
ADAPT = adaptation period allotted to the predator
CATCH = catching a prey item
COIN = coincidence in space
D- = density
DIST = distance between predator and prey
DM- = diameter
ENLARG = factor accounting for the enlargement of the gut size
FC- = food content
FDEPRT = time period of food deprivation
-FI = food intake
FINTIM = finishing time of the simulation
FT = feeding time
-G = gut
-GE = gut emptying
GUTC(ON) = gut content
H- = handling
HANDLE = handling a captured prey
I- = initial
M- = mean
N- = number
OPT- = optimum
PART = partial ingestion (vs. WHOLE)
PN = predation rate
PRC = probability of a prey capture
PST = steady state probability
PT = p(t)
PTD = p(t + DELT)
PY = food content of the prey
R- = rate
RDRAW = random drawing using the random number generator
-REP = replicates
REPDEL = time delay of prey replacement
REPR = reproduction
-RES = resorption

RR- = relative rate
RSA = rate of successful attack (excluding feeding time)
RSE = rate of successful encounter (including feeding time)
-RW = predator is resting and prey is walking
S- = sum
SD = satiation deficit
SEARCH = searching for prey
SR- = success ratio
TEMP = temperature
TSC = time spent per successful capture
V- = variance
VL- = velocity
VP = velocity of the predator
-W = weight
WHOLE = complete ingestion of the prey content
-WR = predator is walking and prey is resting
-WW = predator and prey are walking

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