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Simple Order of Prey Preference Technique for Modelling the Predator Functional Response

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ABSTRACT

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The predator functional response to several prey types and densities may be conceptualized as a multi-dimensional version of the one-dimensional Holling functional-response curves; however, this empirical approach requires inordinate amounts of data to develop and test. A simulation method of modelling this functional response is to consider the behavior of a predator faced with the choice of several prey types. In this model, when all prey are available the predator's selection will depend on the absolute abundance of the most-preferred prey type, irrespective of the abundances of the less-preferred prey types. Consequently, the predator will consume only the most-preferred prey types while that type is available in sufficient numbers. When abundance of the most-preferred type declines below a certain level, the predator will begin to include in its diet the second-most-preferred prey type along with the most-preferred prey type. This order-of-preference technique holds up well when the model is compared to population data from *Oligonychus pratensis* (Acarina: Tetranychidae)/*Neoseiulus fallacis* (Acarina: Phytoseiidae), and is consistent with optimal foraging theory. Implementation is simple, and the data requirements are reduced to determining the predator's order of preference and normalizing the nutritional values of the prey types to a single type.

INTRODUCTION

Work by Huffaker et al. (1963), Rabbinge (1976), Rabbinge and Hoy (1980) and others showed that complex ecological processes may be studied using acarine prey-predator systems. These papers illustrate Logan's (1982) contention that hypotheses and assumptions about a system can be effectively orga-

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nized and tested through the process of model-building and analysis. Another acarine system that is small enough to allow study of several population processes and interactions is that of spider mites and their associated predators on monoculture maize. As a first step toward modelling this system, we developed a prey-predator model of Banks grass mite *Oligonychus pratensis* (Banks), and its predator, *Neoseiulus fallacis* (Garman). The life-history parameters were available from the literature (Allawi, 1983; Congdon and Logan, 1983). However, predation by *N. fallacis* on the multiple-life-stage prey *O. pratensis* was unknown and posed a theoretical and practical problem. The predation component was needed as a first step in our plans to later build a comprehensive temperature-dependent model for theoretical and management applications. Therefore, our primary objective was to find a simple and reliable technique for simulating prey selection by a multiple-life-stage predator consuming a multiple-life-stage prey.

Several authors have dealt with the problem of predator selectivity by application of theoretical, mathematical models (Gurtin and Murphy, 1981; Hastings, 1983). An extension of Holling's (1959) concept of predator functional response to prey density has been proposed as a multi-dimensional functional response to prey life-stage densities (Lawton et al., 1974; Hassell, 1978; Fernando and Hassell, 1980). The amount of data needed to estimate the parameters that Hassell (1978) proposes is enormous. Alternative methods for estimating predatory-mite selectivity have been used in simulation models with varying degrees of success (Fransz, 1974; Rabbinge, 1976; Dover et al., 1979; Rabbinge and Hoy, 1980; Sabelis, 1981; Shaw, 1982).

Several problems are associated with estimating the functional response in the laboratory. One involves predator movement out of a patch. At low prey densities the predator, in nature, is likely to leave a patch in search of higher prey densities where locating prey is more efficient. However, in laboratory experiments, the predator normally is not allowed to leave the patch. Forcing the predator to search at prey densities below its threshold for leaving a patch may result in what appears to be a Type II functional response even when the underlying response is Type III (Van Lenteren and Bakker, 1976). The size of the experimental universe can also affect the functional response (Takafuji and Deguchi, 1980). Another important factor is changes in prey densities during the experiment due to consumption by predators or reproduction by ovipositioning prey. These changes in prey density may confound the measurement of predation rate. Additionally, the predator's attack rate as a function of hunger may not be in equilibrium with the experimental prey density. Consequently, the length of the experimental time period may be critical.

In our work, we approached the problem of accurately determining the form of the functional response by considering the behavior of an individual predator searching for prey. Using this approach we have developed a model that mechanistically simulates the predator's response to given prey types, and thus

allows hypotheses about searching behavior, switching, and the functional response to be addressed. Empirical treatments of predation can obscure mechanisms and require large amounts of data. Our goal was to focus on the individual so that we could gain insights into the process of predation in this system, and to develop a more simple and effective simulation model.

MODEL DEVELOPMENT

Assumptions and model structure

Our initial model was developed for homogeneous conditions and therefore does not include any driving variables, such as temperature and humidity. A constant temperature of 26 °C and a relative humidity above 70% are assumed. There is neither emigration nor immigration by either prey or predator. The prey population is limited only by predation and otherwise exhibits exponential growth. The predator population is limited only by the number of prey available. All motile predator life-stages, except adult males, consume prey. The immature stages starve at the same variable rate as the adults in times of prey scarcity. All prey individuals above refuge levels are equally available to the predator.

The model (Table 1; Fig. 1) has two main components, the prey submodel and the predator submodel. Within these submodels calculations are performed for predation (DIET); predator oviposition (PRDOVI); and predator starvation (ADSTRV). The lower row of rectangular boxes (Fig. 1) represents the prey life-stages developing (from left to right) to the adult stage (BADULT). Individuals move out of each life-stage into the next life-stage or move into the mortality sink at rates relative to the magnitude of the state variables. Additional mortality flows to the sink (due to predation) are controlled by information flows from DIET. Eggs flow from the source at a rate relative to the number of adults present.

Growth and natural-mortality flows for the predator are similar to those for the prey and are represented by the upper row of rectangular boxes. Information flows from the predator life-stages to the DEMAND calculation. The result of the DEMAND calculation is sent to DIET along with information flows from the prey (number of mites in each life-stage). Information concerning total number of mites consumed along with the number of adult predators is passed to PRDOVI and ADSTRV. PRDOVI is a relative rate used with the number of adult predators to control the flow of predator eggs from the source to AEGG. Likewise, ADSTRV is a relative rate which controls the mortality flows for all the predator motile life-stages.

Individual ovipositional predators in this system have been shown to be much more important as consumers than are immature predators (Allawi, 1983). As a result, the model was first built without including the immature predators.

TABLE 1

Parameter and variable definitions

AADULT	state variable of *N. fallacis* adult females	1.0	⟨number of mites⟩
ASEX	*N. fallacis* sex ratio	0.63	⟨proportion female⟩
ALDEM	*N. fallacis* ovipositional female average daily consumption of prey eggs	16.0	⟨eggs/mite/day⟩
ADLINX	conversion factor for Banks adult females to eggs	1.67	⟨eggs/adult⟩
ADSTRV	*N. fallacis* death due to starvation	V	⟨mites/mite/day⟩
AEGG	state variable: *N. fallacis* eggs	V	⟨number of eggs⟩
ADEUT	state variable: *N. fallacis* deutonymphs	V	⟨number of mites⟩
ALARVA	state variable: *N. fallacis* larvae	V	⟨number of mites⟩
APRE	state variable: *N. fallacis* preovipositional females (includes males)	V	⟨number of mites⟩
APROTO	state variable: *N. fallacis* protonymphs	V	⟨number of mites⟩
BADULT	state variable: Banks adults	V	⟨number of mites⟩
BDEUT	state variable: Banks deutonymphs	V	⟨number of mites⟩
BEGG	state variable: Banks eggs	V	⟨Number of eggs⟩
BGMSEX	Banks sex ratio	0.61	⟨proportion female⟩
BLARVA	state variable: Banks larvae	V	⟨number of larvae⟩
BMALE	state variable: Banks adult males	V	⟨number of adult males⟩
BNYMPH	state variable: Banks nymphs	V	⟨number of nymphs⟩
BPRE	state variable: Banks preovipositional females	V	⟨number of preovi mites⟩
BPROTO	state variable: Banks protonymphs	V	⟨number of mites⟩
DAADUL	*N. fallacis* adult natural mortality	0.1	⟨mites/day⟩
DBADUL	Banks adult natural mortality	0.086	⟨mites/day⟩
DBEGG	Banks egg natural mortality	0.04	⟨mites/day⟩
DEMAND	predator demand for prey	V	⟨egg equivalents/day⟩
DT	time-step	0.1	⟨day⟩
DEUDEM	*N. fallacis* deutonymph average daily prey egg consumption	5.0	⟨eggs/mite/day⟩
EGGDEM	Banks egg equivalents demand by ovipositional predators	16.0	⟨eggs/day⟩
LARCON	Banks larvae consumed	V	⟨larvae/day⟩
LARINX	conversion factor; Banks larvae to eggs	0.58	⟨eggs/larva⟩
LARDEM	*N. fallacis* larval average daily consumption of prey eggs	1.64	⟨eggs/mite/day⟩
MXOPT	*N. fallacis* maximum oviposition rate at 26°C	4.0	⟨eggs/day/*N. fallacis* adult⟩
NYMCON	Banks nymphs consumed	V	⟨nymph/day⟩
NYMINX	conversion factor; Banks nymphs to eggs	1.2	⟨eggs/nymph⟩
PRODEM	*N. fallacis* protonymphal average daily consumption of prey eggs	4.48	⟨eggs/mite/day⟩
PRODMX	Banks egg equivalents required by the predator for maximum reproduction	16.0	⟨eggs/mite/day⟩

TABLE 1 (continued)

PRDOVI	variable, calculated reproduction rate of *N. fallacis*	V	⟨eggs/day/*N. fallacis* adult⟩
PRYOVI	Banks oviposition rate	0.82	⟨eggs/Banks adult female/day⟩
RADEUT	*N. fallacis* deutonymph developmental rate to preovipositional female	0.99	⟨mites/mite/day⟩
RAEGG	*N. fallacis* egg developmental rate to larva	0.82	⟨eggs/egg/day⟩
RALARV	*N. fallacis* larva developmental rate to protonymph	0.99	⟨mites/mite/day⟩
RAPRE	*N fallacis* preovipositional female developmental rate to oviposition	0.99	⟨mite/mite/day⟩
RAPROT	*N. fallacis* protonymph developmental rate to deutonymph	0.99	⟨mite/mite/day⟩
RBDEUT	Banks deutonymph developmental rate to preoviposition	0.62	⟨mites/mite/day⟩
RBEGG	Banks egg developmental rate to larva	0.34	⟨mites/eggs/day⟩
RBLAR	Banks larva developmental rate to protonymph	0.62	⟨mites/mite/day⟩
RBNYM	Banks nymph developmental rate to adult	0.35	⟨mites/mite/day⟩
RBPRE	Banks preovipositional female	0.84	⟨mites/mite/day⟩
RBPROT	Banks protonymph developmental rate to deutonymph	0.74	⟨mites/mite/day⟩
REFADL	Banks refuge level for adults	100.0	⟨adult prey⟩
REFEGG	Banks refuge level for eggs	0.0	⟨eggs⟩
REFLAR	Banks refuge level for larvae	100.0	⟨larvae⟩
REFNYM	Banks refuge level for nymphs	100.0	⟨nymphs⟩
RESMIN	minimum number of prey eggs for predator basal metabolism	4.0	⟨prey eggs/day/ovipositional predator⟩
STRV	*N. fallacis* starvation parameter	0.64	⟨mites/mite/day⟩
STRVDLY	amount below EGGDEM needed for predator to 'feel' hunger for counting switch delay	5.0	⟨prey eggs/day⟩
TCON	total prey egg equivalents consumed/day	V	⟨eggs/day⟩
TCONAF	total prey egg equivalents consumed* predator adult female/day	V	⟨egg*mite/day⟩
TDEM	total demand for prey (same as DEMAND, which is altered in DIET)		
YNGRP	Predator immature death due to starvation	V	⟨mites/mite/day⟩

'V' signifies a calculated variable.

Instead, individuals were moved directly from egg to the adult stage. However, that approach was inadequate because the time delays that the different life-stages represented were needed to correctly simulate mite developmental rates. Also, without predation by immatures, the magnitude of the state variables was consistently higher than those observed in the microcosms (Fig. 4). Although the ovipositional predator consumes at least five times more than any

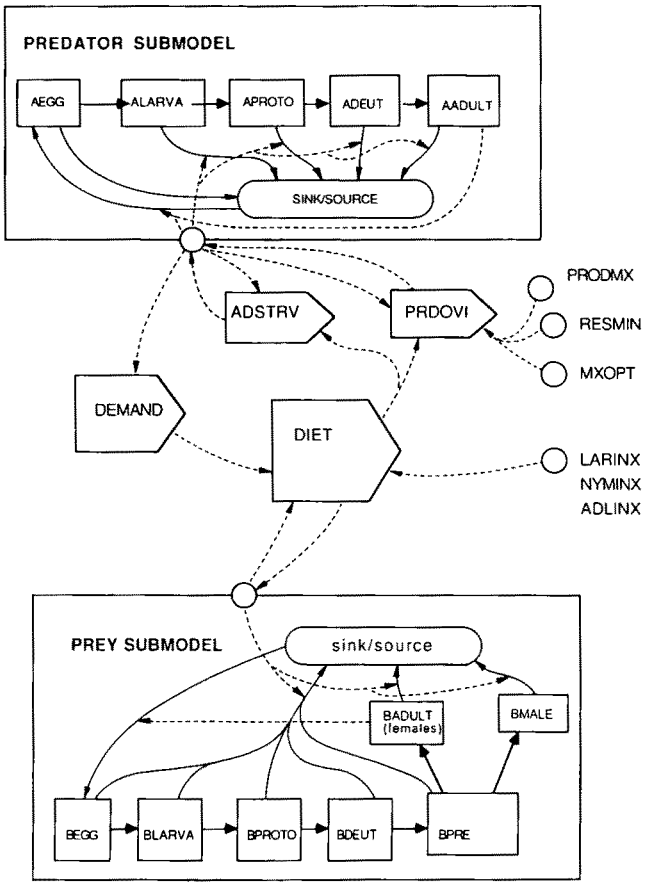

Fig. 1. Conceptual diagram of the model structure. Rectangular boxes indicate state variables; five-sided boxes, computational controls; circles, input variables. Solid arrows indicate flows of material or changes of state: dashed arrows indicate controls or computational transfers. ADSTRV, predator starvation rate; DEMAND, total predator population demand for prey; DIET, diet selection subroutine; PRDOVI, predator oviposition rate; PRODMX, prey egg equivalents required by the predator for maximum reproduction; RESMIN, minimum number of prey eggs for adult predator basal metabolism; MXOPT, predator maximum oviposition rate at 26 °C; LARINX, NYMINX, and ADLINX, conversion factors for prey larvae, nymphs and adults to prey-egg equivalents, respectively.

other life-stage (Allawi, 1983), the combined predation by the more numerous immatures is essential in simulating the mite system.

Finite difference equations are used to represent the system because rates were measured at discrete intervals. Consequently, the time step (DT) is considered a parameter. *Oligonychus pratensis* life history parameters were cal-

culated from data reported by Congdon and Logan (1983). *Neoseiulus fallacis* parameters were calculated from data of Allawi (1983).

Rate variables

The values of the rate variables ADSTRV (Fig. 2) and PRDOVI (Fig. 3) are dependent on the amount of prey consumed. To determine ADSTRV, no starvation is assumed when the consumption rate equals RESMIN (the number of prey eggs needed to just maintain an ovipositional predator but not allow oviposition). RESMIN is assumed to be equal to the egg consumption rate of a preovipositional female. When the consumption of prey egg equivalents/adult female predator (TCONAF/AADULT) falls below RESMIN, the starvation rate (ADSTRV) is equal to the proportion of RESMIN not met, multiplied by the

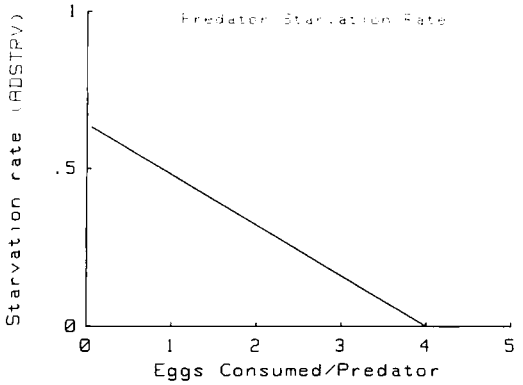

Fig. 2. Predator daily starvation rate (ADSTRV) plotted as a function of prey egg equivalents consumed per predator.

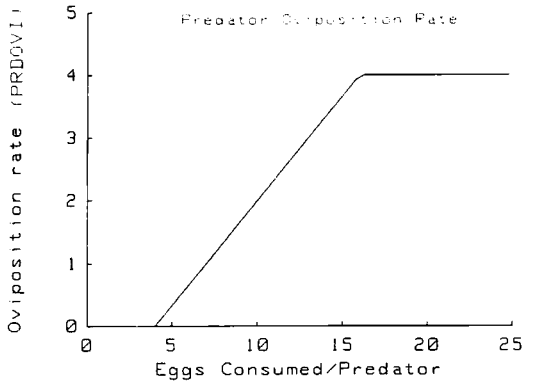

Fig. 3. Predator daily oviposition rate (PRDOVI) as a function of prey egg equivalents consumed per predator.

starvation rate of ovipositional females in the complete absence of prey (STRV) (Allawi, 1983). Consequently, if no prey were consumed ADSTRV would equal STRV; this relationship is shown in Fig. 2. ADSTRV is also used as the starvation rate for immature predators.

Oviposition (Fig. 3) is maximized for *N. fallacis* when the consumption rate equals PRODMX (set at 16 *O. pratensis* eggs/(day*ovipositional *N. fallacis*); Allawi, 1983). Oviposition is zero when consumption of prey egg equivalents is less than or equal to RESMIN (set at 4; Allawi, 1983). When consumption is greater than or equal to PRODMX then the oviposition rate is set to the maximum rate (MXOPT). When consumption falls between RESMIN and PRODMX the ovipositional rate is calculated as a proportion. The total consumed (TCONAF) minus the total needed for adult maintenance (AADULT*RESMIN) is divided by the total needed for maximum oviposition less the amount needed for maintenance (AADULT*(PRODMX−RESMIN)).

DEMAND is calculated by summing the products of the number of individuals in each predator life-stage, multiplied by their corresponding demand for prey egg equivalents.

Subroutine DIET

To determine the predation on each prey life-stage we have used a simple and direct approach that avoids the problems associated with an empirical estimation of the functional response. This mechanistic technique is based on the predator's strong preference for prey eggs and for the smaller life-stages (Burnett, 1970, 1971; Croft and Blyth, 1979; Allawi, 1983; Berry, unpublished data, 1983). The algorithm is as follows; a prey life-stage refuge level (the prey density at which the predator will add to its diet a less-preferred life-stage) is subtracted from the total number of prey in each life-stage to obtain the number of prey available. The prey refuge makes some of the prey in a life-stage unavailable to the predator. The prey life-stage refuge levels are only important when predators are very numerous relative to the prey. Predators are most abundant around the time prey begin to decline. During each time-step the predator first consumes all of the prey items (above the life-stage refuge level) in the most-preferred stage. If the predator has not met its nutritional needs it proceeds to add to its diet the second-most-preferred life-stage and so on, until it is satiated or runs out of available prey.

This approach is similar to the predatory redshank's response to less-preferred prey; Goss-Custard (1977) reported that the redshank's selection of less-preferred prey was dependent on the absolute density of the more-preferred prey rather than relative density of the prey types. Absolute abundance of more-preferred prey types has also been important in the diet selection of other predators such as the shore crab (Elner and Hughes, 1978), great tit

(Krebs et al., 1977), bluegill sunfish (Werner and Hall, 1974) and for an optimization model (Estabrook and Dunham, 1976).

Assumptions of the order-of-preference technique are that a predator has equal probability of finding any given prey stage, and time does not limit a predator's ability to find prey during each time-step. During model development we discovered that the predatory mite does not begin to include less-preferred life-stages immediately after the numbers of the most-preferred life-stage become too low to meet the predators' demand. Consequently, a 1-time-step delay was added to the model so that predators initially include less-preferred prey items 1 time-step after DIET indicates. At the time predators in the simulation begin to consume prey larvae (second-most-preferred stage), all refuge levels are set to zero because the predator searches much more effectively, perhaps due to increased walking speed.

Parameter estimation

Predation on prey life-stages was calculated by standardizing each prey life-stage to prey-egg equivalents using the conversion factors LARINX (larvae to eggs), NYMINX (nymphs to eggs) and ADLINX (adults to eggs). LARINX, NYMINX, and ADLINX are calculated by dividing the average daily consumption of prey eggs (Allawi, 1983) by the average daily consumption of larvae, nymphs and adults (Allawi, 1983), respectively.

Phenological development is simulated using a distributed delay after Mantesch (1976) and Rabbinge (1976). Rates of development and rate of death due to ageing were calculated from the lengths of the developmental periods and longevity of the adults respectively, using the following equation:

$$M=(1-r)\exp(T) \tag{1}$$

which yields

$$r=1-\exp((\ln M)/T) \tag{2}$$

where r is the rate to be calculated (animals/day), T is length of the developmental period (longevity for adults) in days, and $M=0.1$ ($0.0<M<1.0$, represents the proportion of animals remaining at the end of T days).

As individuals develop into the next life-stage, the number of individuals in the current life-stage will approach zero exponentially and asymptotically, assuming no recruitment. Therefore, M must be greater than zero and must reflect a mean residence time in each life-stage. An M that is too small will cause the model to move the mites through the developmental stages too fast, whereas $M=0.1$ produced reasonable results given the number of substages used in the model.

The time-step DT, which is a parameter in difference-equation models, was selected by testing various time-steps in the model. A time-step which is too

large can cause erratic behavior. The time-step should correspond to the rate parameters, which represent data collected at discrete intervals, such as an hour or a week. Consequently, information is lost when a time-step is selected that is much smaller than the sampling interval for data collection. The percent change of a state variable during each time-step is the critical factor. Innis (1979) suggested that a state variable not change more than 20% during a time-step as a general guideline for selecting the magnitude of the time-step. A time-step of 0.1 day satisfied the 20% guideline, and therefore was used in all simulations. Table 1 lists parameters and their values.

MODEL VERIFICATION

Several simulations were run to test the model in cases where the results were predictable beforehand. For example, predator starvation may be tested by setting the prey state variables to zero to see whether the predator population dies and, if so, how long it takes. Ovipositional predators were reduced to 10% of their original numbers in 5 days when the prey state variables were set to zero. Laboratory data indicate that the ovipositional predator starves in 3–7 days (Allawi, 1983). As expected, the model allowed no predator reproduction under these conditions.

Prey adult longevity was tested by setting PRYOVI (prey ovipositional rate) and all state variables, except prey adults, to zero. This test showed that prey adults decreased to 10% of their original numbers after 26 days, as reported by Congdon and Logan (1983).

Prey numbers increased exponentially ($r_m = 0.27$) when predators were absent. The rate calculated directly from life-table data (Congdon and Logan, 1983) was $r_m = 0.23$. Predators increased exponentially ($r_m = 0.36$) when an overabundance of prey were present. Predator life-table data were unavailable so an observed r_m could not be calculated.

Adult predator longevity was tested by setting MXOPT (predator maximum ovipositional rate) and all predator immature stages to zero and setting the prey state variables large enough to ensure an overabundance of food for the predator. Predators declined to 10% of their initial numbers in 22 days under these conditions. This is consistent with laboratory experiments where ovipositional predators lived for 20–25 days (Allawi, 1983).

A stable age distribution produced by the model for *O. pratensis* was similar to the stable age distribution for spider mites reported by Carey (1983). In the simulation, the predator will always kill all of the prey, given enough time. After all prey are killed, all life-stages of the predator decline rapidly to zero.

MODEL VALIDATION

The model was validated by comparing model results to data from the biological system that were simulated by the model. These data were collected

from laboratory microcosm experiments on whole maize leaves. Greenhouse-reared, 4–6-week-old maize host plants were used for these experiments. Each experiment consisted of *O. pratensis* and *N. fallacis* confined to a single leaf. A band of Tack Trap® adhesive at the proximal end of the leaf prevented ambulatory emigration by the mites from the experimental leaf. However, aerial dispersal could not prevented. The experiments were conducted in environmental chambers at 26°C with light:dark (L:D) 16:8-h photoperiod. An open pan of water was placed in the bottom of the chamber to raise the humidity high enough (70% r.h.) to allow predator reproduction.

Adult female *O. pratensis* were placed on the maize leaf and allowed to oviposit for 24 h. These adults and their eggs were counted under a dissecting microscope so that exact numbers at the start of the experiment were known. Ovipositional predators were transferred with a camel's-hair brush from the laboratory colony to the maize leaf and were not deprived of food prior to the experiment. Model simulations began with these initial numbers of mites. Adult female *O. pratensis* and *N. fallacis* were counted once every 24 h using a 10× hand lens. Some adult female *N. fallacis* escaped from the microcosm. Since emigration was not accounted for in the model, individuals that had emigrated were subtracted from the simulated population on the day that they were discovered missing.

Figure 4 shows graphs of the microcosm data-sets and corresponding simulation results. Five of the seven microcosm data-sets are simulated with reasonable accuracy, especially regarding general trends. However, the model generally over-estimated predation and predator numbers during the decline phase.

Initially, adult prey declined slightly in the simulation due to natural senescence, with no recruitment into the adult stage during the first 4 days of the experiment. This small reduction is an artifact of analog-type behavior of the distributed-delay technique, and shows that adult prey were not being attacked by the predator. However, the predators were ovipositing and consuming prey during this time so that by day 4 there was recruitment into the predator adult stage. The ensuing rapid decline of adult prey is associated with the point when the predators began to include in their diet adult prey in response to low densities of the more-preferred prey life-stages (eggs and immatures). The model predicted the onset of this decline phase in most cases. This is consistent with optimal foraging theory (Krebs, 1979), which predicts that predator selectivity is dependent on the absolute density of the more-preferred prey type, not on its relative density to less-preferred prey types. Figures 4a and 4f are exceptions that may indicate that other factors can contribute to prey selection or that prey selection may have a large random component.

The model results and microcosm data both indicate that adult female prey are not consumed until the density of the more-preferred prey items is low. However, the simulated predation on the adult prey and predator numerical

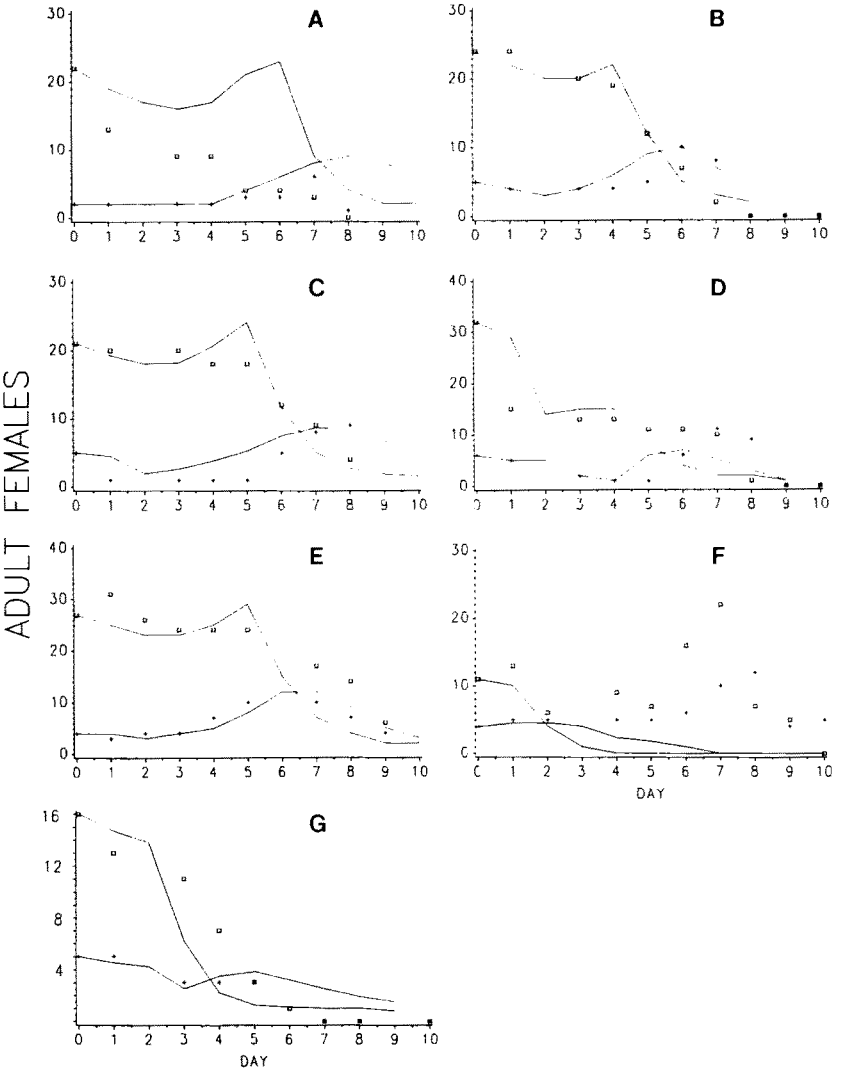

Fig. 4. Validation data and simulation results (solid lines) for seven microcosm experiments. Adult female prey are represented by squares, and adult female predators by plus signs.

response at low prey densities were much greater than in the microcosm. At low prey densities, the assumptions that all prey are equally available and that time does not limit the predator's ability to find prey might be incorrect. The predators may not be able to find the prey needed during a given time-step DT. A stochastic prey refuge level while prey are at low densities may help solve this problem by 'hiding' a few prey from the predator. Stochastic refuge levels

probably should be constructed so that predators have a high probability of finding all of the prey over an extended period of time.

The model failed to simulate the behavior of the system in two cases (Fig. 4a, f). In Fig. 4f the model did well for the first 2 days but was aberrant from then on. The model was constructed so that adult female prey were consumed only when all other prey life-stages were not present in sufficient numbers to satiate the predators. Consequently, when predators in the model began to consume adult prey there were almost no other prey available. The result was a rapid decline of adult prey in the simulations. In the microcosm data of Fig. 4f, the prey population did not continue to decline after the time when predators began to consume adults (indicated by the decline of prey adults on day 2). Instead, prey numbers began to increase for several days, indicating that the predators were behaving in an unusual way. For example, if several predators stopped consuming prey and laying eggs but remained alive (e.g. developed into the postovipositional stage or became diseased) after day 2, the prey population could have recovered, as seen in Fig. 4f.

From Fig. 4a it appears that adult prey were consumed by the predator earlier than the model predicted. Alternatively, the prey mites may have left the leaf either aerially by spinning down on silk threads or by being knocked off when the plants were handled. Therefore, the assumption of no emigration would have been broken. Another factor that may have influenced the results from this microcosm is that, unlike all others, there were no prey eggs present at the beginning of the experiment. Therefore, the 1 time-step delay for predators to include less-preferred prey items may not have been appropriate.

SENSITIVITY ANALYSIS

Sensitivity analysis establishes the relative influence on model output of changes in various input parameters (Wiens and Innis, 1974) and can be an important tool for evaluating the structure of a model. Innis (1979) suggested that a-priori intuitive estimates of sensitivity be compared to the actual model sensitivity to the parameters. Any disagreement between the two can lead to discovery of model coding errors, incorrect model structure, or new insight into the biology of the system. Conversely, such comparisons may also serve to support hypotheses concerning the biology of the system and the model's representation of it.

A second use for sensitivity analysis is as a tool to determine the needed accuracy for the parameters. Sensitivity analysis facilitates concentrating data collection efforts on parameters that have the most influence on model behavior. Finally, if the model represents the biology of the system, sensitivity anal-

ysis can give a measure of the reaction of the system to changes in a given parameter (Wiens and Innis, 1974). This is an important property of simulation models.

To perform the analysis, a parameter or small groups of parameters were perturbed by $\pm 1.0\%$ while holding all other parameters constant. Model results from the altered inputs were compared to the results from an unaltered or control input set of parameters. The control parameter values, which were the same as those used in the model validations, are listed in Table 2. Several parameters were evaluated in groups because they were closely related (e.g. developmental rates) or because they represented a single process or concept, like predator demand for prey.

Because the long-range objective of our modelling effort is to provide a tool for estimating the likelihood of a predator bringing an agricultural pest under control in a particular field situation, we chose three sensitivity indicators that would be potentially useful in an agricultural system. These were: MAXPRED (% change from the control to the sensitivity runs in the maximum number of adult predators); MAXPREY (% change from the control to the sensitivity runs in the maximum number of adult prey); and PDATE (% change from the control to the sensitivity runs in the time at which the prey were maximum). Only adult prey were used because they are larger and, thus, typically the only life-stage counted by field scouts. Also, the maximum number of prey (phytophagous mites) could be used as an indicator for the amount of damage caused by the prey before they are brought under control by the predators. Predatory-mite abundance relative to prey-mite abundance could be used to predict how soon the predator will control the prey in a given field. MAXPRED, MAXPREY and PDATE are reported in Table 2. Values for MAXPRED, MAXPREY and PDATE less than the percent change in the parameters (1.0%) show that the model is insensitive to small changes in the altered input parameter. Values of 1.0% indicate that the magnitude of the change in the model result is equal to the magnitude of the change of the input parameter.

In general, MAXPREY was more sensitive to parameter changes than MAXPRED. For example, MAXPREY showed maximum sensitivity of 6.9% to perturbation of the parameters for prey life-stage developmental rates, whereas MAXPRED showed a maximum sensitivity of 6.4%. MAXPREY and MAXPRED were moderately sensitive to changes in the sex ratios of both the predator and prey (Table 2) because sex ratios determine the reproductive potential of both species. In addition, the demand for prey eggs by the predator was affected by changes in the sex ratio because the adult female predators constitute an important prey consumer. Generally, MAXPREY was more sensitive to parameters associated with the prey and predator numerical responses (developmental and ovipositional rates, sex ratios, and adult longevity) than to the parameters which affect predator functional response (Table 2). Thus, the model indicates that the predator's numerical response is a major factor in this system. These relationships are similar to those reported by Shaw (1982) for another mite

TABLE 2

Results of the sensitivity analysis

Description		Parameter	Control value	Perturbation	MAXPRED	MAXPREY	PDATE
Predator reproductive rates		RAEGG	0.82				
		RALARV	0.99				
		RAPROT	0.99	+1.0%	−4.5%	−4.9%	−1.4%
		RADEUT	0.99				
		RAPRE	0.99				
Daily predator stage demand for prey eggs	adult	ADLDEM	16.00				
	larva	LARDEM	1.64				
	nymph 1	PRODEM	4.48	+1.0%	−3.7%	−2.6%	−0.7%
	nymph 2	DEUDEM	5.00				
	preovi	PREDEM	5.72				
Minimum number of prey eggs to maintain an adult predator		RESMIN	4.0	−1.0%	−0.2%	0.0%	0.0%
Prey reproductive rates		RBEGG	0.34				
		RBLAR	0.64				
		RBPROT	0.74	+1.0%	+6.4%	+6.9%	−1.4%
		RBPDEUT	0.62				
		RBPRE	0.84				
Predator daily demand for prey eggs for maximum oviposition		PRODMX	16.0	−1.0%	−0.1%	−0.1%	0.0%
Conversion factors: prey life-stages to prey egg equivalents		LARINX	0.95				
		NYMINX	1.20	+1.0%	+0.6%	+0.3%	+0.7%
		ADLINX	1.67				
Predator sex ratio: M/F		AASEX	0.63	+1.0%	−3.8%	−3.7%	−0.7%
Prey sex ratio: M/F		BGMSEX	0.61	−1.0%	−3.2%	−3.4%	0.0%
Predator death rate due to starvation		STRV	0.64	+1.0%	−0.2%	0.0%	0.0%
Predator maximum oviposition rate		MXOPT	4.0	−1.0%	+4.2%	+4.4%	+1.4%
Predator adult state variable		AADULT	1.0	+1.0%	−2.5%	−2.5%	−0.7%
Prey adult state variable		BADULT	30.0	+1.0%	+3.8%	+3.6%	+0.7%
Time step		DT	0.1	+1.0%	+0.2%	+0.4%	+0.3%
Prey oviposition rate		PRYOVI	5.00	−1.0%	−6.1%	−5.8%	−0.7%
Prey egg natural mortality		DBEGG	0.04	+10%	−0.3%	−0.2%	0.0%
Predator adult senescence rate		DAADUL	0.1	+1.0%	+0.9%	+1.3%	+0.7%
Prey adult senescence rate		DBADUL	0.086	−1.0%	+1.5%	+1.9%	+0.7%
Predator developmental and oviposition rates		MXOPT	4.0				
		RAEGG	0.82				
		RALARV	0.99	+1.0%	−8.1%	−8.8%	−2.8%
		RAPROT	0.99				
		RADEUT	0.99				
		RAPRE	0.99				
Predator:							
Maximum oviposition		MXOPT	4.0	+1.0%			
Prey eggs needed for maximum oviposition		PRODMX	16.0	−1.0%	−3.9%	−3.8%	−0.7%

The indicators are MAXPRED, MAXPREY and PDATE, the percent change from the control run in the maximum numbers of the predator, prey and the date of prey maximum number, respectively.

predator/prey model. In contrast, MAXPRED was more sensitive than MAXPREY to the parameters that affect the predator functional response (daily egg demand, prey life-stage to egg conversion factors). MAXPRED was most sensitive to the prey reproductive rates (RBEGG, RBLAR, RBPROT , RBDEUT, RBPRE, PRYOVI).

The date of maximum numbers of prey (PDATE) was fairly sensitive to the reproduction parameters of both species. However, PDATE was less sensitive to the input parameters than were MAXPRED or MAXPREY (Table 2).

The prey were also more sensitive to the adult prey senescence parameter DBADUL than were the predators. This was probably related to changes in prey fecundity as a result of increasing or decreasing the longevity of ovipositional prey females. For example, as predator numbers increase in the simulation and become somewhat limited by prey abundance, the predator ovipositional rate begins to decrease. This may be exacerbated by decreased prey fecundity. The resulting reduction in the predator numerical response near the prey peak may allow prey levels to be higher in the sensitivity run during the decline phase.

Some life-history attributes are affected by several input parameters simultaneously. For example, numerical response is influenced by both ovipositional and developmental rates. In order to analyze the combined effect of parameter groups, two sets of interacting parameters were evaluated for sensitivity. The first such parameter group influenced the predator numerical response and consisted of predator maximum ovipositional rate (MXOPT) and predator developmental rates (RAEGG, RALARV, RAPROT, RADEUT, RAPRE). These parameters produced little synergistic interaction in the model. The other set of interacting parameters was associated with predator oviposition and included MXOPT ($+1.0\%$) and the number of prey needed for maximum predator oviposition (PRODMX; -1.0%). As expected, these alterations increased the predator numerical response and thus caused the predators to kill all of the prey sooner; this was illustrated by the negative values for PDATE, MAXPRED and MAXPREY in Table 2. The decreases were less than additive for MAXPRED and even less so for MAXPREY and PDATE which indicates the importance of nonlinearity in the system.

CONCLUSIONS

Our modelling effort provided some insight into the mite system it was designed to simulate and into multiple life-stage systems in general. The order-of-preference technique we developed appears to be effective and allows the multiple life-stage predation model to be much simpler. Also, data requirements for our model were less than for the empirical approaches. Data requirements were reduced because our mechanistic approach only required determining the predator's order of preference, prey refuge levels, and normalized nutritional values of the prey life-stages.

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