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SIMULATION OF THE INTERACTIONS OF PREDATORY *TYPHLODROMUS* MITES WITH THE EUROPEAN RED MITE, *PANONYCHUS ULMI* (KOCH)

D. L. Johnson[1] and W. G. Wellington

Institute of Animal Resource Ecology, University of British
Columbia, Vancouver, Canada, V6T 1W5

INTRODUCTION

In 1982, we completed a series of field and laboratory studies on the roles and interactions of weather, predation, and dispersal in an orchard mite system in the Okanagan Valley of British Columbia. The species most intensively studied on two apple cultivars, McIntosh and Delicious, were the European red mite (ERM) *Panonychus ulmi* (Koch), and two of its phytoseiid predators, *Typhlodromus caudiglans* Schuster and *T. occidentalis* Nesbitt (Johnson, 1983).

Since there is conflicting evidence concerning the ability of these phytoseiids to provide reliable control of *P. ulmi* populations within intensively managed orchards, we were particularly interested in their relative abilities to reoccupy trees from which they had been eliminated by pesticides or other means. The field studies therefore included a variety of removal and exclusion experiments to provide details of within- and between-tree methods of dispersal by the prey and its predators at different stages of their life cycles.

Most of the field results will be published later. We have used some here, however, to construct a simulation model of the interactions of *Typhlodromus* spp with *P. ulmi* (Fig. 8). This model takes into account field demonstrations (Johnson, 1983) that *T. caudiglans*, in particular, rarely moved among or between trees and the ground cover, either by air or via the trunk. In contrast to this slow dispersal of its predators, *P. ulmi* actively dispersed within trees (and throughout the orchard when the weather was suitable) thereby frequently imparting to this otherwise unstable natural system a stability comparable to that demonstrated in other mite systems by Huffaker (1958), Huffaker et al. (1963) and Takafuji (1977). We constructed our research model to explore further population consequences of these differences in dispersive ability.

SYSTEM SIMULATION

Relationship to Other Mite Models

Phytoseiid-tetranychid predator-prey systems have received a great deal of atten-

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[1] Present address: Agriculture Canada Research Station, Lethbridge, Alberta, Canada, T1J 4B1.

tion because of the economic damage attributed to tetranychids and the potential for their control by phytoseiids. LOGAN (1982) and WELCH (1979) have summarized mite predator-prey simulation models. Two models of the interaction of the European red mite and phytoseiid predators have been published. DOVER et al. (1979) simulated the relationship of the ERM to *Amblyseius fallacis* in Michigan orchards, with innovative approaches to spatial distribution and its effect on predation. RABBINGE (1976) produced a highly-detailed state-variable simulation of the ERM and phytoseiid mites, principally *Amblyseius potentiallae.* He provided a detailed sensitivity analysis and field validation.

T. occidentalis has received considerable attention in computer simulation, though not in relation to the ERM. FRANSZ (1974 a, b) simulated the functional response of *T. occidentalis* to *Tetranychus urticae* prey via a detailed component analysis. His findings and the CSMP model of RABBINGE (1976) have been adapted by RABBINGE and HOY (1980) to a simulation of these species. LOGAN (1977) simulated the interaction of *T. occidentalis* with *Tetranychus mcdanieli,* via a specialized simulation language (SIMBUG) and a general model for temperature-dependent rate phenomena. Further effects of differential temperature-dependent growth in this system were modelled by WOLLKIND and LOGAN (1978). RABBINGE and SABELIS (1980) and SABELIS (1981) published the results of simulations of several species of tetranychids and phytoseiids, and provided detailed models of walking behavior, reproduction and predation by phytoseiids. Population growth of the ERM in the absence of phytoseiids has been modelled by HERNE and LUND (1979).

Although they are cast in a variety of computer and simulation languages, these models have the same basic form. All follow a state-variable structure in which state descriptions of the populations of interest are changed in relation to internal and external variables. Within this framework a wide variety of approaches to particular functional relationships is apparent.

Our model summarizes the ecology and interaction of the ERM and *Typhlodromus,* in order to explore the potential effects of prey dispersal in the absence of predator dispersal. The results identify areas for which more empirical information on the form and behavior of components is required. A complete listing of the model program, written in FORTRAN, can be provided by the authors on request (see also Fig. 8).

The European Red Mite Submodel

Life History. The ERM hatches from diapausing "winter eggs" in the spring. The larvae begin feeding on young apple leaves and within days become protonymphs, then deutonymphs, and finally adult males and females. One generation (egg to egg) takes about three weeks, depending on the weather and time of year. There are five to nine generations a year. Under decreased photoperiod in August and September, winter eggs, which require chilling before they will complete development and eclosion, are laid.

We modelled this life cycle by beginning a year with a development vector of winter eggs from the previous year. In a one-year run of the model, this vector is initialized at 1000 winter eggs. The eggs may be of similar developmental status, or may be distributed over 20 levels of completed development, as described in the following section.

Development. The temperature-dependent rate of development of mites appears to be non-linear within the temperature range experienced under field conditions (TANIGOSHI et al., 1975a, b; LOGAN et al., 1976; HERNE and LUND, 1979). In cases in which development rate is a reasonably linear function of temperature, degree-day summations can be used to simulate development (FRAZER and GILBERT, 1976). In general, however, a different approach to integrating development is required. Since developmental rate is a function of temperature and temperature is a function of time, we must integrate

$$\int_{t_1}^{t_2} R(T(t))dt.$$

The integral can be approximated by assuming that temperature is constant for small time intervals, say one hour. This general approach is commonly employed in models of arthropod development (e.g., RUESINK, 1976; LOGAN, 1977; HERNE and LUND, 1979; RÉGNIÈRE, 1982).

The rate of development of winter eggs of the ERM was estimated by measuring the number of days required to hatch at three fluctuating temperatures. A group of 316 winter eggs, collected December 29, 1981, from the UBC Experimental Orchard, was randomized among three growth cabinets programmed to reproduce smooth sine temperature functions with an amplitude of 5°C, period of 24 h, and mean temperatures of 10°, 15° and 20°C. The number hatched was counted once a day and the larvae removed. Hatching time as a function of temperature (Fig. 1) was similar to the results of TROTTIER and HERNE (1979), but times required to hatch were considerably longer than those reported by HERBERT and MCRAE (1982). Time in days required to hatch is described by a least-squares fit to the 316 hatch times:

$$\text{Days}=\exp\left[5.0326-0.10225\ (\text{Temp.})\right]$$
$$r^2=0.836 \quad F_{1,314}=1598. \quad (p<.0001)$$

The experiment was repeated and the equation above verified by comparison with the hatch times of over 13,000 winter eggs collected on April 13, 1982, at the Okanagan Valley Summerland Research Station. The same non-linear functional relationship was apparent, with adjustment for heat experienced during early April. TROTTIER and HERNE (1979) give physiologic time to 50% hatch as 155 degree-days above 5.6°C. Although this linear estimate gives a reasonable prediction (Fig. 2 correctly predicts a hatch around the end of April) the fitted equation as applied in

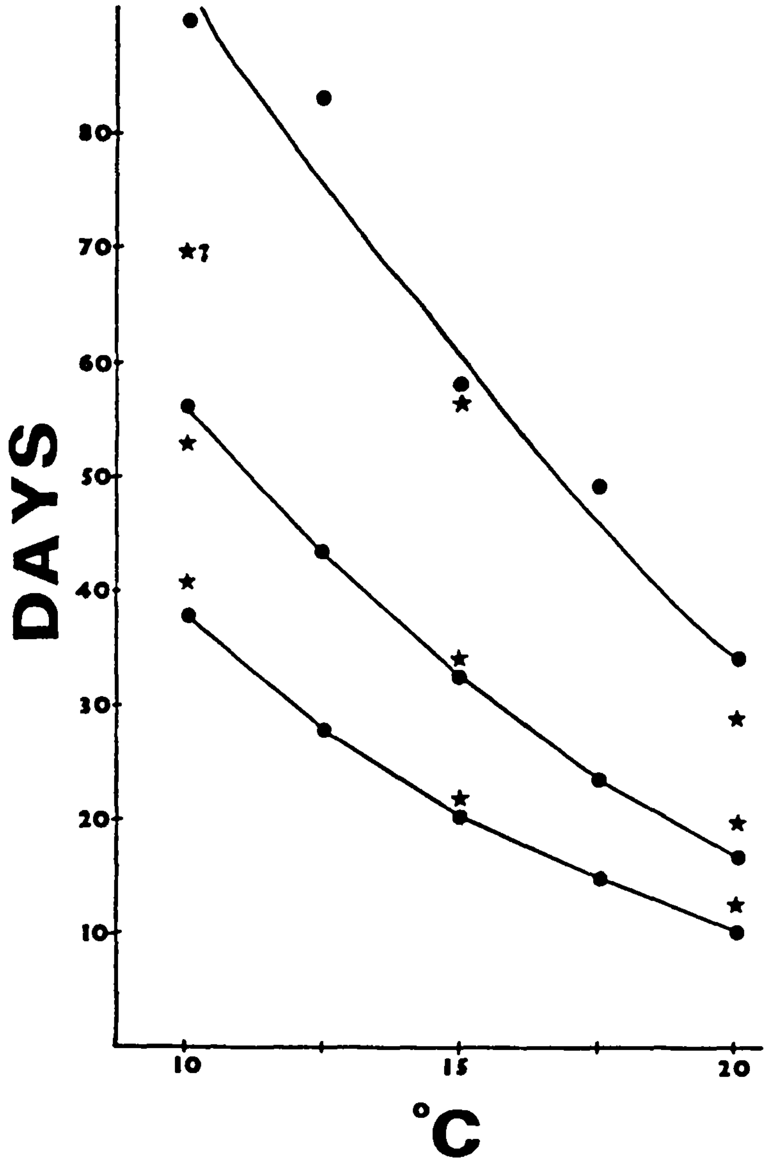

Fig. 1. Days required for ERM winter eggs to hatch as a function of temperature. Times until first hatch (bottom line), 50% hatch (middle line) and last hatch (top line) are shown. The graphs are based on data from TROTTIER and HERNE (1979), with our observations indicated by stars. The "?" indicates that observations were not continued past 70 days.

the model gives a better dynamic description of hatching with no increase in computation or complexity.

Developmental functions of summer eggs and active mites from hatch to maturity did not differ significantly from those reported by HERNE and LUND (1979), so their exponential equations were used in the model. Field temperatures measured in

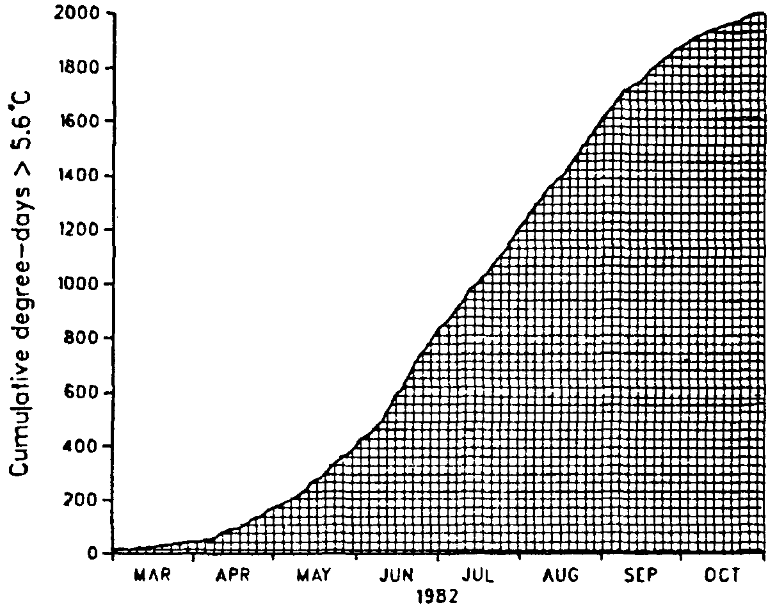

Fig. 2. Degree-days above 5.6°C. Temperatures measured in the Summerland experimental orchard.

the Summerland orchard in 1982 were used in the model to calculate hourly development rate from a sine function fitted to the daily maximum and minimum temperatures. Developmental vectors in the model consist of 20 positions (Fig. 3), and contain as elements the number of mites that have completed up to $i/20$ of their development ($i=1, 2, \ldots, 20$), that is 0-5%, 5-10%, and so on up to 95-100% of the development for that stage. The daily development, calculated from the integration discussed above, is summed and the developmental vector updated. For example, if the weather allows 17% of summer egg development to be completed on a particular day (one time-step), then the elements of the summer egg vector are advanced forward 3 positions (i.e., INT (.17/.05)), leaving 3 positions free at the bottom and advancing the top 3 positions into hatcher status. The remainder (2% in this case) is saved and added to the next day's development. Once development is calculated for the next stage (juveniles), they are moved forward the appropriate number of positions, and the hatching eggs are merged into the open positions available at the bottom of the juvenile vector, preserving the age structure of the hatchers. Thus the problems of different rates of growth by different stages and of hatching occurring at different times of the day are accounted for (see Fig. 3). A similar result is achieved by a slightly different method in LOGAN's (1977) simulation system.

Fecundity. ERM adults are parthenogenetic (arrhenotokous) but apparently rarely go unmated in nature, since all-male families have not been found. Females lay up to 5-6 eggs per day, but usually 1-3 per day, depending on temperature and female age. Females usually live 18 to 22 days. After a preovipositional period of 2.5-3.5

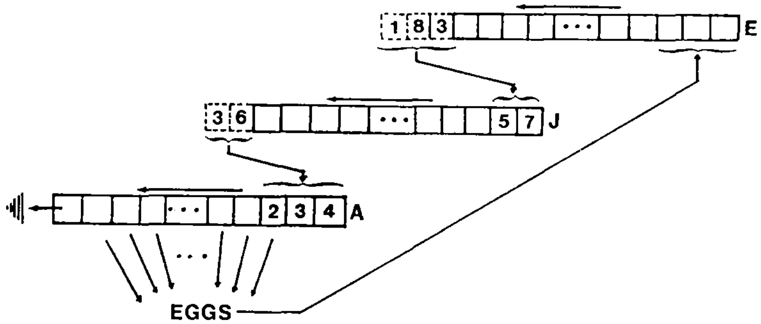

Fig. 3. The method of updating the egg (E), juvenile (J) and adult (A) developmental vectors of the ERM. The method of merging transfers is described in the text.

days, they lay 10 to 46 eggs over a period of 12-16 days (CAGLE, 1946; HERBERT, 1981). In the model, the first two positions in the adult age vector are pre-ovipositional adults; egg-laying begins in the third position. The fecundity function, shown in Fig. 4, was fitted by eye to data from RABBINGE (1976). Data from our laboratory colonies were not as extensive, but indicated that fecundity did not increase much above 25°C, so an asymptotic effect of temperature on fecundity was used in the model. Field temperatures used in the model rarely exceeded 30°C.

Winter egg production begins August 1. A small proportion of females are devoted to laying winter eggs in early August, and this proportion increases in a typical logit manner to 50% of the females by mid-September and nearly 100% by mid-October. Females of later generations lay fewer eggs than females earlier in the year. The sex ratio used in the model was 70% female through the summer.

Mortality. A multiple regression equation fitted to data from RABBINGE (1976) was used to give approximate adult mortality rate as a function of age and temperature.

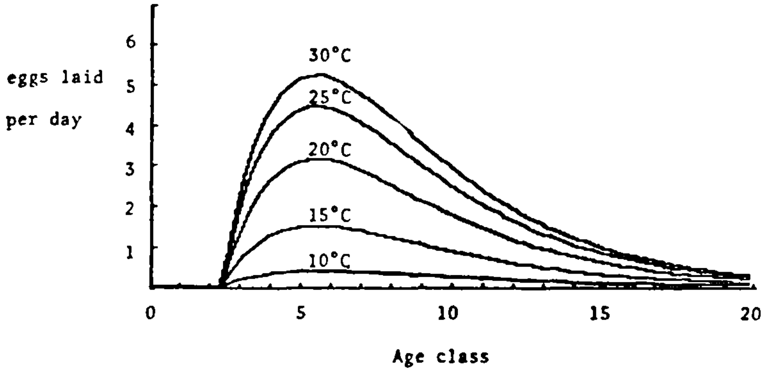

Fig. 4. The ERM fecundity function used in the model. The first three age classes represent pre-ovipositional adult females. RABBINGE'S (1976) data on age- and temperature-dependent oviposition rates were intitially used in fitting the function.

Winter eggs, summer eggs and immature stages suffer daily mortality of 1%, 1% and 2% respectively.

Predation by *Typhlodromus*

Most of the phytoseiids present in the 1982 field experiments were *T. caudiglans*, with some *T. occidentalis* and rarer species present. Since their life histories are reasonably similar (PUTMAN and HERNE, 1964; RABBINGE, 1976), life history parameters for both species are freely mixed. Data and/or parameter estimates on development, predation and fecundity were obtained from LAING (1969), LEE and DAVIS (1968), LOGAN (1977), PUTMAN (1962), TANIGOSHI et al. (1975 a) and SABELIS (1981), and verified where possible by experiments in growth cabinets or plastic mite cages on apple leaves in the Summerland orchard. In some cases, we made assumptions concerning the effects of temperature and other factors (e.g., search rate is an unknown function of temperature, so we used a function that would give a reasonable functional response, rather than assume that temperature has no effect). LOGAN's (1977) developmental function for immature *Typhlodromus* was incorporated into the model. An exponential function describing aging of the adults was fitted to data from TANIGOSHI et al. (1975 a).

The FRAZER and GILRBET (1976) model of the functional response of predation to prey density, as formalized by GUTIERREZ and WANG (1977)[1], was used in the model. The number eaten during one interval of time is described by:

$$E=N(1-\exp(-(bP/N)(1-\exp(-aN/b))))$$

where N=prey available

E=total number eaten in one timestep (1 day)

P=number of predators

a=predator search rate (a fitted constant)

b=maximum predator demand per timestep (1 day)

Good data on the functional response of *Typhlodromus* predation to ERM density are lacking. In our laboratory tests, the largest number of protonymphs eaten in one day by a single adult *Typhlodromus* was 14 at 25°C. The mean predation at this temperature was 8.5 per day. At 10°C, predation rates were highly variable, and adults ate between 0 and 7 per day. Reported predation rates on other tetranychids are near this range (LOGAN, 1977; PUTMAN and HERNE, 1964; SABELIS, 1981). We assumed that search rate (a) and predator demand (b) were asymptotic functions of temperature, reaching practical maxima of 0.03 and ~13 near 30°C. Figure 5a illustrates estimated predation at 20°C for a range of predator densities. Figure 5b illustrates the increase in predation rate with temperature. The predation parameters may also be functions of predator age and experience (EVELEIGH and CHANT, 1981 a,

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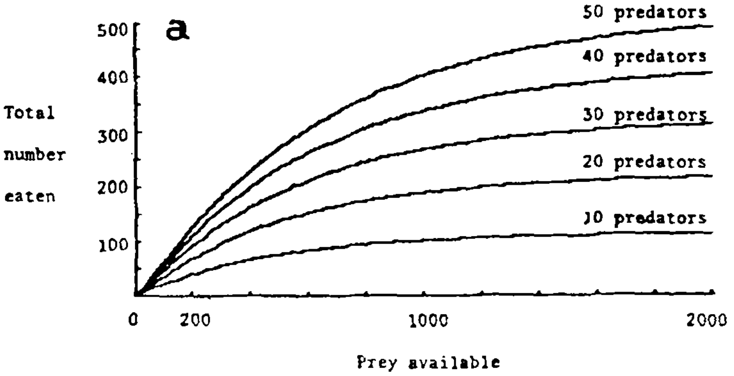
[1] A typographical error appears in this equation in GUTIERREZ et al (1980). The 1977 version is correct.



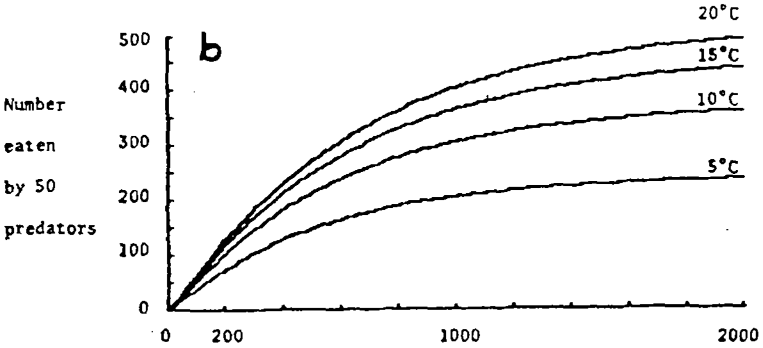


Fig. 5. (a) The family of curves produced by the Frazer-Gilbert model (Gutierrez and Wang, 1977) parameterized at 20° in the present model. (b) The effect of temperature on the predation function.

b), but these are not included in the model in its present form.

Typhlodromus caudiglans larvae do not feed, and nymphs and adults rarely eat eggs or adult ERM (Putman and Herne, 1964). Winter eggs are not eaten. The model assumes that the effects of predation by *Typhlodromus* act on the juvenile stages of the ERM, and that the numerical response of the predator depends on the availability of juvenile prey (ERM larvae, protonymphs and deutonymphs). A two-day running average of the number eaten per predator is used to determine predator fecundity and survival rates.

Adult female *Typhlodromus* are mated in the fall and overwinter on the trees. A low fecundity (0.2 eggs per day per adult) is possible in the early season, even without prey. *T. caudiglans* normally lays up to 1 egg per day (Putman, 1962; Putman and Herne, 1964), depending on the number of prey eaten. Fecundity of 0.5 eggs per day occurs at 5 prey eaten per day, and approaches 1.0 as the number of prey eaten increases. Mortality of adult predators is based on the number of prey eaten, and time required to starve to death depends on the temperature (predators live longer at cooler temperatures).

Spatial Relationships

The theoretical aspects of dispersal and its effects on populations were first addressed by SKELLAM (1951). HUFFAKER's (1958) experiments stimulated interest in the effects of animal movement and spatial relationships on predator-prey systems. Subsequently, a great deal of attention has been given to the problem (reviewed by HASSELL, 1978, 1980; LEVIN, 1976, 1977; MURDOCH and OATEN, 1975). Most of this attention has been theoretical in nature. A large number of recent studies concern the effects of predator and prey dispersal along gradients or between patches on the stability of model populations (e. g., COMINS and BLATT, 1974; CROWLEY, 1981; GURNEY and NISBET, 1978; HASTINGS, 1977, 1978; HILBORN, 1975, 1979; HOGEWEG and HESPER, 1981; MIMURA and MURRAY, 1978; RENSHAW, 1982; ROFF, 1974; SMITH, 1974; VANDERMEER, 1973). Most of these models either ignore within-patch dynamics and consider only the rate of prey-patch appearance and disappearance, or are variants of typical LOTKA-VOLTERRA models. Although these models are quite artificial, they usually support one generalization: increasing spatial complexity and/or prey dispersal increases persistence of the system, given a low predator dispersal rate and a heterogeneous environment. Very low relative rates of dispersal of the predator lead to predator extinction in most models.

Unfortunately, adding spatial components and animal movement to even moderately complex simulations can increase their complexity and running time enormously (as in the case of the spruce budworm model: CLARK, 1979; HOLLING, 1978). Other ways of adding dispersal are needed. LOGAN (1982) emphasizes this need:

> "Development of methods to efficiently model the interactive dynamics of age-structured populations dispersing through a heterogeneous environment may result in a third generation of prey-predator models. Such models... will provide insights which are at least as great as the previous two generations of models..., the analytic models of population ecology and computer simulation models."

Rather than model a single isolated tree as a representative "average" of system behavior, and thereby exclude dispersal, or ignore the admonitions of CLARK (1979) and plunge into the large-scale computation and complexity needed to model an entire orchard, we used a simplified approach to this problem. The model considers a single tree within which dispersal is unrestricted and homogeneity is assumed. A switch is supplied which will allow random dispersal of female red mites to and from the tree. When there is no dispersal, the ERM population on the tree is determined by the initial numbers of winter eggs in the spring, the daily temperatures supplied over the year, and the action of the predator, if present. When dispersal occurs (i. e., when the dispersal switch is "on"), each day n migrants ($-1<n<1$) are added to m randomly chosen adult ERM age classes (1 to 20). The number of migration events, m, can be varied. Early versions of the model used 10-20 such transfers per simulated day, but we found that even low numbers of dispersers had striking results on the interaction of *Typhlodromus* and the ERM. The effects of within-tree, clumped or random distributions are not considered in the model.

Temporal Considerations

The time-step is one day for all processes other than development, for which hourly rates are summed. Variable time-steps are not useful in this case; there are no long periods of little change, since generations are frequent and partially overlapping. One run of the model is one growing season, April 1 to October 31. Field temperatures for 1982 are used in the model. (Temperatures from other years could be used if adjustments were made for differences in orchard and weather station temperatures. Since winter eggs are laid in the fall of each run, runs could easily be strung together to simulate successive years, though the model has not been used in this way. It has not been "tuned" to reproduce field observations, since it was constructed to examine the gross behavior of the system, while maintaining realistic age-structure and development (JOHNSON, 1983). Since it is a vehicle for preliminary examination of the ecology of orchard mites, its present form is not meant for use in management, although with additional parameter estimates, field validation, and minor adjustments, it could serve that purpose).

BEHAVIOR OF THE MODEL

The ERM Submodel

This submodel has the initial values of the state variables set to simulate the mite population on one branch; e. g., it begins April 1 with 1000 winter eggs. The scale is not so important as the general behavior, but the following graphical output can be considered to represent the mite population on one moderate-size branch, or 50-100 leaves.

Given a vector of maximum and minimum orchard temperatures, the unadjusted ERM submodel behaves very much like unrestricted populations might (Fig. 6). The oscillations are the result of the multivoltine life history of the ERM (the model contains no stochastic terms or predation at this point). Winter eggs begin hatching after mid-April and continue to do so until the end of May, with the 50% hatch occurring around the second week of May. Juveniles appear by March 1, and result in a first generation of adults peaking near the end of May. This result agrees very closely with previous field records and experiments in 1982 (JOHNSON, 1983). Since the only connection between the model and the field observations is the vector of daily temperatures, we can conclude that this simulation of ERM development is successful.

The model output exhibits 6 complete generations, with a weaker 7th in October. Adult peaks lag juvenile maxima by 1-2 weeks. There are 6 generations of summer eggs; the 7th generation of females, and a proportion of the 6th, are devoted to

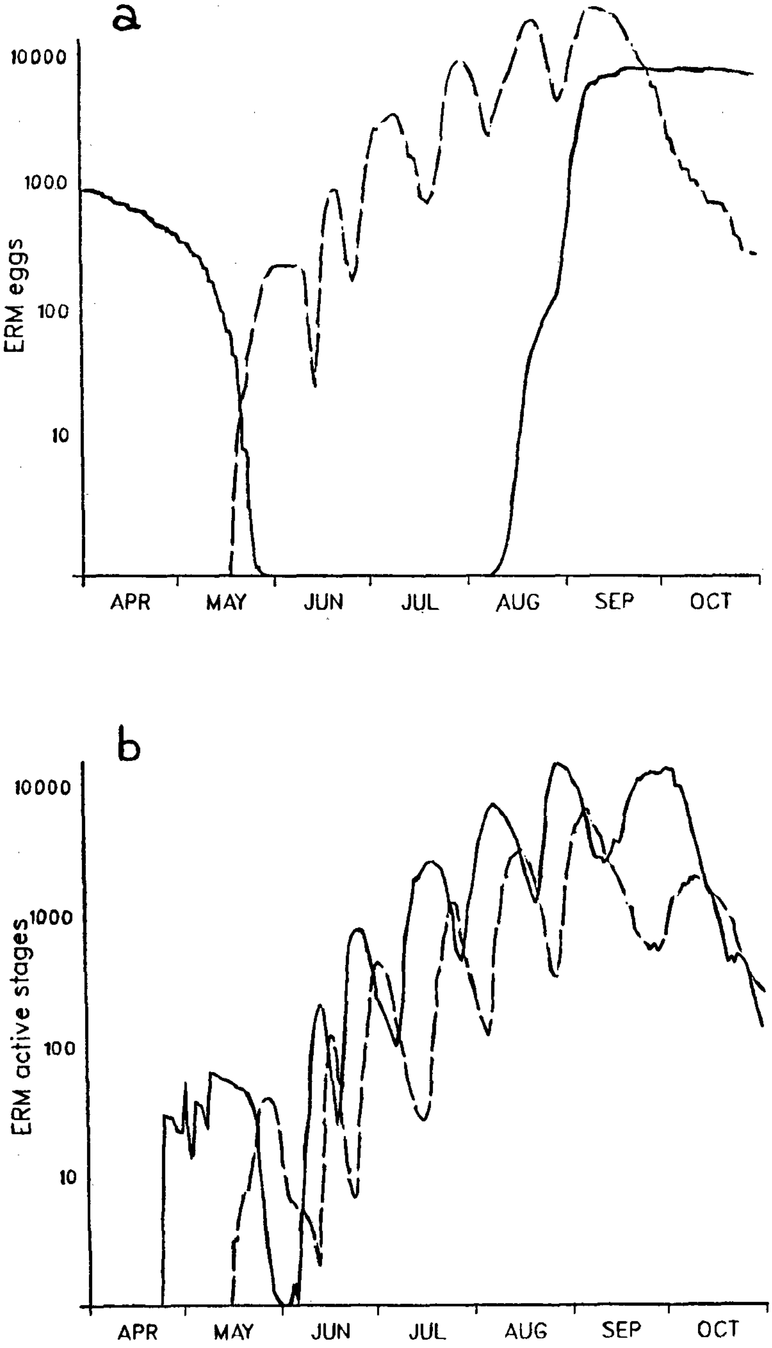


Fig. 6. ERM population growth (a) and age structure (b) predicted by the model. No predation or dispersal are included in this run. In (a) dotted line shows summer eggs; solid line, winter eggs; (b) juveniles, solid line; adults, dotted line.

production of winter eggs. Winter eggs are produced from early August to October, and by the end of the summer more than enough have been laid to produce a similar population the following year. Parameters determining winter egg production and mortality would need refinement if this model were to be used to simulate a series of successive years. Although the late-season decline in the number of active mites does not begin until September in the model output, actual ERM populations exhibit a decline after July or August (see also DOWNING and MOILLIET, 1967, 1972; HOYT, 1969). This decline in the field populations occurs even in the *absence* of phytoseiid mites (JOHNSON, 1983 and in lit.). Since moderate decline in female productivity over the summer is included in the model, this discrepancy between real and simulated populations may be due to any of several factors: 1) actual reduction in fecundity after midsummer may be much more than expected; 2) other predators, such as *Zetzellia mali* and *Campyloma verbasei*, may cause significant late-season declines; and 3) emigration from the trees may be extensive in late summer, when lighter winds and warmer temperatures encourage the aerial dispersal of young adult females (JOHNSON, 1983). (This last explanation has also been invoked by NISHINO (1976; cited in TAKAFUJI, 1980) to explain a similar decline in *Panonychus citri*).

Sensitivity to Temperature

The basic ERM submodel's sensitivity to temperature was tested with three runs at temperatures above and three runs at temperatures below the standard 1982 field temperatures. In the six runs, $-3, -2, -1, 1, 2,$ or 3 was added to the daily maximum and minimum field temperatures. The "$T+3$" run produced an unrealistically large ERM population by midsummer, with no apparent separation of generations after June. Because the model in its present form contains no density-dependent self regulation of the ERM, the population density thus can rise to extreme values under such very warm conditions. Since a 3°C increase across the year is unnaturally high, and since the model has been constructed with the British Columbia climate in mind, we have omitted this high temperature treatment in the subsequent analyses and discussions.

Effects of Dispersal

The importance of dispersal on stabilizing predator-prey systems is well-established (HILBORN, 1975). Here we examine its effect on predation at the meso-scale of a single patch; i.e., one tree, with immigration and emigration.

When predation is added to the ERM submodel, the *Typhlodromus* population starts at typically moderate to high levels (adult females overwinter on the tree and emerge from cracks and scars on the bark in early spring), but dies out by the first of June. This trend occurs over a wide range of justifiable predation, fecundity and mortality parameter values. Although this result may seem unrealistic, it is in keeping with the early-season declines apparent in the 1982 field data. It would be possible to "force" the modelled predator population to survive through this early period, but a better solution can be achieved by incorporating prey dispersal into the model. When the dispersal switch is "on", adult prey migrate to and from the modelled system after May 20. Figure 7 illustrates the resulting indirect effect of this dispersal ($-1<n<1$; $m=10$) on the ERM adult female populations via the predator: the predator survives into July, and significantly reduces prey populations over this longer period.

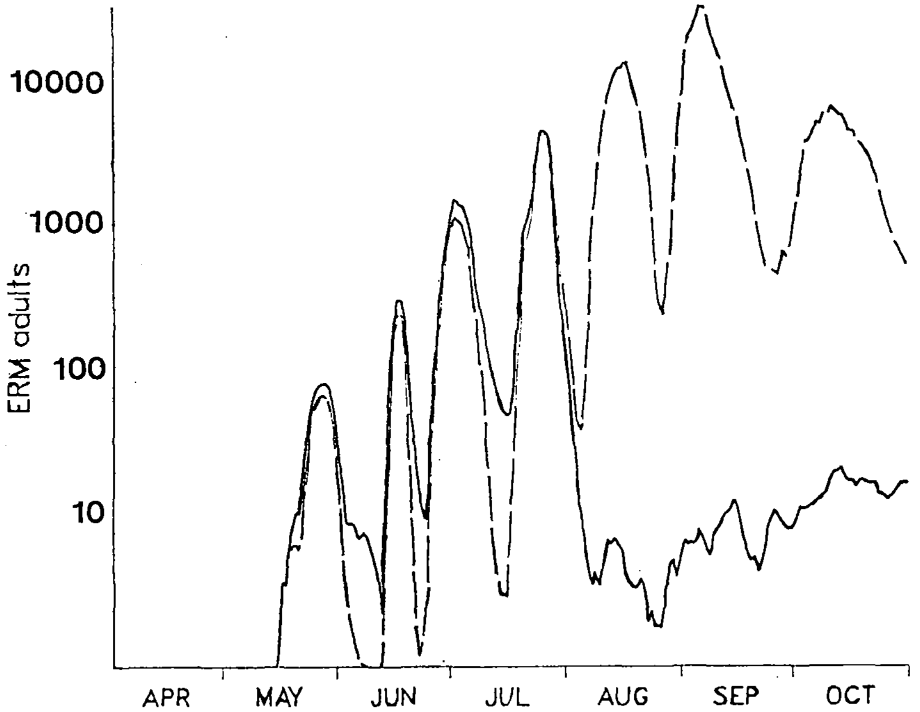


Fig. 7. The consequences of including dispersal and predation (at field temperatures). In this run, the predators survive and impose mid- and late-season control of the ERM when dispersal is *added* (solid curve vs dashed curve in which there was no dispersal).

The ability of the predator to suppress the prey during this period is quite sensitive to numerical and functional responses. In standard runs, maximum predator fecundity did not exceed 1.0 egg per female per day, and maximum realized predation was less than 10 prey juveniles per adult day. Greater refinement of these functions, and adjustments of the parameters (based on further experimental estimates of the predators' responses), therefore would be required before this research model could be a reliable management tool.

Incorporating the dispersal (immigration and emigration) of adult ERM females in the present model, however, smoothed the otherwise violent fluctuations in juvenile prey early in the season (Fig. 7) and thus reduced predator starvation and/or losses in potential fecundity. Since all these processes are temperature-dependent, dispersal should have different effects under different temperature regimes.

Interaction of Dispersal and Temperature

At extremely low rates of adult prey dispersal ($-1<n<1$; $m=3$; i. e., an average of 0, and up to 3, adult prey invading the branch each day), predator populations cannot quite survive through the critical early period. The outcome, however, is temperature-dependent. The results of runs with low dispersal at "$T+2$", "$T+1$", "$T+0$", "$T-1$", "$T-2$" and "$T-3$"°C showed that, in two cases, "$T-1$" and "$T-3$"°C, the predator population persisted and significantly reduced the ERM. At "$T-1$", *Typhlodromus* enjoyed a more even supply of suitable prey through May and June, due to slower ERM development, and thus was able to rally sufficiently in July and August to reduce the ERM population. (At temperatures$>T-1$, more rapid ERM development reduced the time during which juvenile prey was accessible.) At "$T-3$", there were fewer prey available in May than at "$T-1$", but survival of the starving predators was sufficiently improved by the cool conditions for them to persist long enough to attain low to moderate levels by late summer. The "$T-2$" run had neither the benefit of increased prey densities in May nor of sufficiently cool temperatures, so the predator died out. However, at this temperature the prey was limited by the cooler conditions and so did not attain the densities exhibited under the higher temperatures, "0", "$T+1$", "$T+2$" and "$T+3$". At the higher temperatures, the phytoseiids failed, and the prey increased unimpeded under the highly favorable growing conditions. Such breakdowns of the biological control of the ERM by *Typhlodromus* are well-known in natural situations.

DISCUSSION

Different types and rates of dispersal have major impacts on population behavior (MORRIS, 1971; MYERS and KREBS, 1971; THOMPSON et al., 1976; WELLINGTON, 1964). Differential dispersal, achieved through differences among age classes, genetic groups, physiological types, or even between haves and have-nots, is an effective means of dealing with a highly unpredictable world (WELLINGTON, 1977, 1980; also reviewed by JOHNSON, 1969; SOUTHWOOD, 1962, 1977; STEARNS, 1976; STINNER et al., 1983). But in predator-prey interactions, inter- as well as intraspecific differences in dispersal rates also arise. As HUFFAKER (1958) demonstrated with his laboratory populations of predatory mites and their prey, the new patterns of dispersion and dispersal generated by such interspecific differences can prevent the self-destruction of otherwise highly unstable systems.

The general importance of dispersal in stabilizing predator-prey systems has been widely recognized since HUFFAKER's pioneer work. Most theorists, however, are still mainly concerned with the population consequences of agile prey emigrating to new habitats ahead of their slower enemies. Only a few (e.g., HILBORN, 1975, 1979) have considered the possible impact of immigrating prey on the whole system, even though there are well-documented field and modelling studies in other research areas that demonstrate the importance of immigrants in very patchy environments (e.g., THOMPSON et al., 1976; WELLINGTON, 1964).

A predator with the extremely slow rate of spread that *Typhlodromus* mites display in natural settings (JOHNSON, 1983) in fact would soon become extinct if its much more rapidly dispersing prey never re-entered recently depopulated localites. But an animal that actively disperses not only emigrates; it also immigrates, re-entering previously denuded patches, adding to sparse or failing populations already there. Without such mid-seasonal replenishment by ERM immigrants, the predaceous *Typhlodromus* in fact regularly die out in field localities where they have exhausted their food supply. Their survival in other patches, and their subsequent success in controlling ERM populations later in the season, thus can be attributed more to their prey's activities than their own.

With animals as small as mites, identifying, or even observing, returning immigrants in field settings can be so difficult that it is not surprising that their existence has been so often overlooked. Other difficulties encountered in natural systems have further obscured the immigration process. In a natural system, one expects to find theoretical consequences of traditional high-prey/low-predator dispersal rates distorted by the interactive effects of population growth rates, predator starvation and weather on the timing and rates of dispersal. Such expectations inevitably help to conceal the intermittent contributions of immigrating prey to the system's stability. Our simulation, in clarifying these contributions, also illuminated another well-concealed field relationship; the weather-dependent nature of prey dispersal (JOHNSON, 1983).

Warm, calm weather not only induces good growth rates among all stages of the ERM; it also encourages young adults to launch themselves from twigs and leaf tips (JOHNSON, 1983). The model confirmed that the increased rates of prey growth and aerial dispersal during such weather reduced inter-tree differences in ERM density, thus replenishing the food supplies of some enclaves of starving *Typhlodromus*. In contrast, warm but windy conditions may contribute to the extinction of such enclaves, since ERM adults then will not launch themselves from leaves, and thus are not dispersed by air currents.

The model showed that such local extinctions of the predator can be delayed by cool weather. In a natural setting, the lower temperatures may keep the predators alive long enough to benefit from the sudden influxes of ERM immigrants that occur when warmer weather again encourages aerial dispersal.

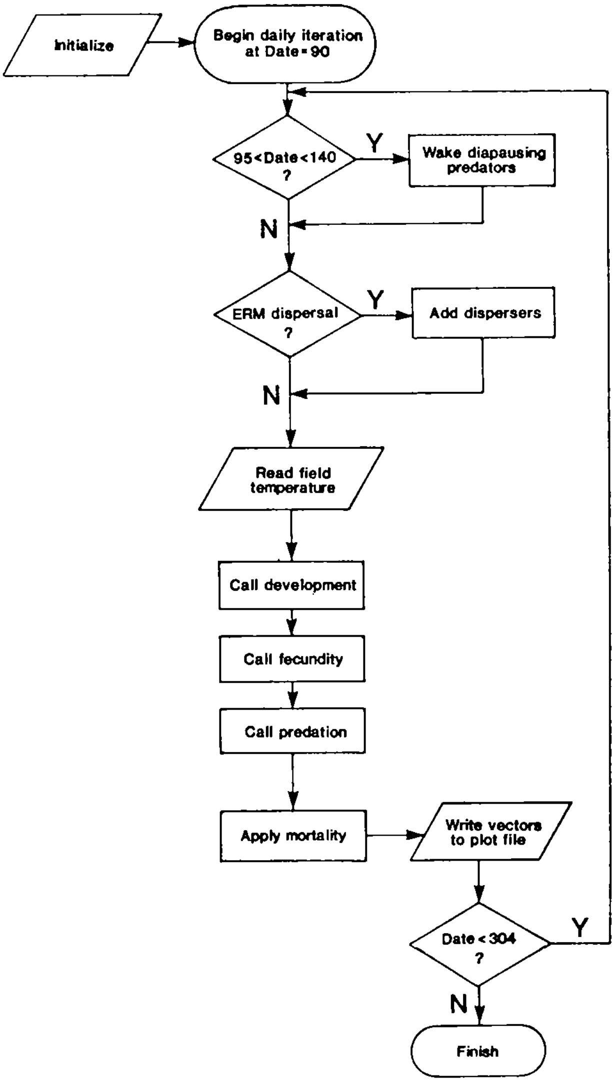


Fig. 8. Flow chart of the mite model's general structure and program sequences.

In a predator-prey relationship in which dispersal of the prey sustains the predator, these powerful interactions of dispersal and temperature can change the fundamental behavior of the whole system. The model has shown the need for further investigation of these effects, to ensure their addition to formal descriptions of predator-prey systems.

SUMMARY

Interactions of *Typhlodromus* mites and their prey, the European red mite, in orchard settings were examined through computer simulation. In particular, the

consequences of very slow dispersal by the predators, compared with the weather-dependent higher rates of prey dispersal, were elucidated. In simulations of the interactions of the predator and its prey, both dispersal and temperature strongly affected the available supply of juvenile prey, and thus could determine whether the predators on an individual tree survived or perished.

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捕食性カブリダニ（*Typhlodromus* 属）とリンゴハダニの相互作用のシミュレーションモデル

D. L. Johnson・W. G. Wellington

果樹園環境における *Typhlodromus* 属の捕食性カブリダニとその餌種であるリンゴハダニとの相互作用をコンピューターシミュレーションの手法によって検討した。特に，ハダニが気象条件に反応して示す高い分散力と，それに較べるときわめて低い捕食者の分散力とが導く結果を明らかにした。シミュレーションの結果，分散と気温の双方が，捕食者が餌として利用できる若齢期のハダニの供給にきわめて強い影響を与え，個々の樹において捕食者が生存しうるか，消滅するのかを，この２つの要因が決めていると考えられた。