Increasing patch connectivity and number reduces attack rates, but does not affect the functional response type of an acarine predator

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Abstract: The functional response is the most basic form of the predator-prey interaction. There are three main response types: a linear rise in prey consumption with increasing prey densities to a plateau (type I), a decelerating curvilinear rise to a plateau (type II), or a sigmoidal shaped curve (type III). Type III responses have been shown to allow for long-term population persistence and be demographically stabilizing, yet type II responses have previously been observed for predators such as the phytoseiid mite *Amblyseius fallacis* when feeding on populations of the spider mite *Panonychus ulmi*. Here, we examine this predator-prey interaction using experimental systems of varying patch number which may more accurately depict the natural environment, and simulations which vary both patch number and connectivity. In no experimental or simulation trial did increasing patch number or connectivity change the functional response of *A. fallacis* from a type II to a type III. Attack rates were lowered with increasing patch number and/or connectivity. Yet, even when dispersal ability was substantially lowered by an 80-fold decrease in connectivity, the functional response remained of type II form. How do predators with this demographically destabilizing functional response persist? Hypotheses regarding metapopulations and alternative prey are discussed.

Introduction

In this study, we examine the effects of varying patch connectivity and number on the functional response, which is the most basic form of the predator-prey interaction. Theory holds that there are three main types of response: a linear rise in prey consumption with increasing prey densities to a plateau (type I), a decelerating curvilinear rise to a plateau (type II), or a sigmoidal shaped curve to a plateau (type III) (Holling 1959). We examined the functional response of the acarine predator *Amblyseius fallacis* (Garman) feeding on *Panonychus ulmi* (Koch). Previous studies have found this predator to have a type II functional response (Croft and Blyth 1979; Lester et al. 1999; Blackwood et al. 2001; Lester and Harmsen 2002). However, this result may be due to the arena on which the functional response is assessed. The difficulty in following small predators such as mites has led most authors to assess the functional response on single, isolated patches. For mites these patches are often small leaf-disks, isolating potential predator and prey movement to a few cm^2. Such analyses may be useful for some comparative aspects of predator-prey ecology, but may not necessarily represent the true functional response of the predator in a natural habitat which is comprised of many individual, but linked patches. Differences in predation as a result of movement between patches may have consequences for the type of functional response and for predator-prey population stability.

Several models and experimental studies have shown the type II response to be destabilizing and not to allow long-term population persistence. In contrast, the type III response has been found to be demographically stabilizing (Hassell and May 1973; Murdoch and Oaten 1975; Hassell and Comins 1978; Nunney 1980; Pech et al. 1992). However, we know that *A. fallacis* and other related phytoseiid species can persist with *P. ulmi* populations in orchards (Parent 1967; Lord 1972; Oatman 1973; Woolhouse and Harmsen 1984; Lester et al. 1998). For this study, our hypothesis was that in systems of multiple patches with varying connectivity, a decrease in the ability of the predator to obtain prey would change the form of the functional response from a type II to a type III response. Such a system containing a set of patches with varying connectivity more closely represents nature than the individual patch or leaf-disk assays previously used to determine the

functional response of these predators. Thus the functional response obtained from such a system may be a more realistic representation of its true shape, which may be of type III form, and which could help explain the observed coexistence of these predator and prey species in orchard systems.

Materials and methods

Predator & prey mite colonies

Panonychus ulmi were reared on seedlings of apple *Malus domestica* Borkhauser, and peach *Prunus persica* (L.) Batsch. These seedlings were maintained at $24 \pm 2°C$, 60% RH and in continuous light. The colony of the predator *A. fallacis* was started in 1993 from mites collected in Jordan, Ontario. The functional response experiments were undertaken in 1997, approximately four years after initiating the colony. Predator colonies were reared in units consisting of a water-soaked sponge within a pie-pan surrounded by a water moat, at $24 \pm 1°C$, 60% RH, and 16 h light : 8 h dark photoperiod. Three times weekly, leaves of the kidney bean infested with the prey *Tetranychus urticae* Koch were added to each rearing unit. The *T. urticae* colony was reared on bean plants, *Phaseolus vulgaris* L., at $24 \pm 1°C$, 60% RH, and 16:8 (L:D) h. Apple leaves with *P. ulmi* were also added approximately once a week in an attempt to circumvent problems encountered when changing the host plant on which predator-prey interactions are observed (Lester et al. 2000).

Functional response experiments

We examined the functional response of adult male *A. fallacis* feeding on *P. ulmi* protonymphs and deutonymphs. Tests were undertaken on 3 cm diameter (total surface area = 7.1 cm^2) apple *M. domestica c.v.* 'Red Delicious' leaf-disks, placed upside-down on wet cotton wool. This leaf size was chosen as it is similar to that of a small leaf while the wet cotton wool restricted the movement of these mites to these leaves. We examined the functional response on a single leaf patch, or two, four or six interconnected leaf patches. To connect the leaf patches, leaves were cut so that they retained a 2.0 cm length of stem. A No. 2 insect pin was inserted at the tip of each stem thereby connecting the leaves before

placement onto the wet cotton wool. All mites were transferred from their colonies onto the apple leaf patches with a fine paintbrush. Experimental arenas were either single or multiple patches, with *P. ulmi* densities in the range of 1- 40 per system. Individual mites were assigned randomly to each patch within the arena. For each *P. ulmi* stage and density, four replicate tests were undertaken. For each replicate, data were collected for one day after two consecutive days of preconditioning of mites to the leaf, prey stage and prey density.

The functional response type of the predators was determined using the methods of Juliano (2001). In a type II functional response the proportion of prey eaten declines monotonically with prey density. However, in a type III (sigmoidal) functional response the proportion of prey eaten is positively density-dependent on prey up to the inflection point of the sigmoid curve, followed by a monotonic decrease. To determine the shape of the functional response, logistic regression was used to predict the proportion of prey eaten, with a dichotomous response variable that equalled 1 for surviving prey and 0 for consumed prey. A polynomial function of initial density was used in the model, that best approximated the relationship of N_e/N_0 to N_0, where $N_e=$ the number of prey eaten, $N_0=$ the initial number of prey available, and thus N_e/N_0 is the probability a prey is eaten. That probability, using for illustration the most general polynomial function we considered, was modelled as:

[Eqn 1]
$$\frac{N_e}{N_0} = \frac{\exp(L_0 + L_1 N_0 + L_2 N_0^2 + L_3 N_0^3 + L_4 N_0^4)}{1 + \exp(L_0 + L_1 N_0 + L_2 N_0^2 + L_3 N_0^3 + L_4 N_0^4)}.$$

Maximum-likelihood estimates of parameters L_0 up to L_4 (as required) were obtained using PROC CATMOD in SAS (SAS 1999). The signs of the coefficients in the polynomial function are typically used to distinguish the type of the functional response (Juliano 2001), with the linear coefficient, L_1, being key: a negative sign indicates a type II response, while a positive linear coefficient indicates a type III response. Higher order terms may be necessary to allow an adequate functional approximation of the data, particularly for Type III responses. We determined the most appropriate order of the polynomial function separately for each experiment, using the small-sample (second order) version of Akaike's Information Criterion, AIC_c, starting with a quartic as our most general approximating model (as in equation 1); see Burnham and Anderson (2002).

Once the shape, and hence the type, of the functional response was determined, nonlinear least squares was used to estimate the parameters associated with the response. As no prey were replaced during the course of the experiment, the appropriate model for a type II functional response is the "random-predator" equation (Rogers 1972):

[Eqn 2] $$N_e = N_0\{1 - \exp[a(T_h N_e - T)]\},$$

where T_h is the time required to handle a prey item, a is the instantaneous searching rate or attack coefficient, and T is the total time prey were exposed to the predators. In a type III response, a is no longer assumed to be constant, but increases with N_0 to an asymptote. The model used to estimate a was the hyperbola, $a = (d + bN_0)/(1 + cN_0)$, where b, c, and d are constants. The type III functional response equation used also accounted for prey depletion (Hassell et al. 1977; Hassell and Comins 1978):

[Eqn 3] $$N_e = N_0\{1 - \exp[(d + bN_0)(T_h N_e - T)/(1 + cN_0)]\}$$

Iterative application of the Gauss-Newton method in PROC NLIN (SAS 1999) was used to estimate the parameters in equations 2 and 3. Type II functional responses were compared in two given populations by using PROC NLIN to solve for N_e the implicit function:

[Eqn 4] $$0 = N_0 - N_0 \exp\{[a + D_a(j)]([T_h + D_{Th}(j)]N_e - T)\} - N_e,$$

where j is an indicator variable that takes on the values 0 and 1 for populations 1 and 2 respectively. The parameters D_a and D_{Th} estimate the respective differences in the values of the parameters a and T_h, between the populations (Juliano 2001). A similar approach is possible for type III responses, but was not required in this study.

Overview of the predator-prey simulation model

An analysis examining the effects of modifying patch connectivity and number on the functional response was undertaken using a simulation model. The model designed for

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this study was an individual, list based model (Fig. 1). For input, individual files are used to simulate the environment, and predator and prey populations. The environmental parameters were initially set to closely resemble the experimental system used in the functional response analysis. In different simulations, predator and prey mites had access to one to six leaf disks of a specified radius. Leaves were "connected" by a section of the leaf edge defined as the "stem". If a simulated individual walks on this section, it was randomly allocated to any leaf in the simulation with a time delay approximating the real movement time for the mites. The area of this leaf edge can be modified, resulting in a probability of movement ranging from very low (with small stem radius), to frequent (with large stem radius).

Data files for the mite populations contain parameters that are relevant to entire predator or prey populations. Parameters in this file include speed, acceleration, the rate of turning or change of direction, the time until speed changes, time until a change in direction, and the time to transit between leaf disks or patches. For the predators, these files also contain data associated with consuming prey. These parameters are the time for a predator to recognize a prey item, the time associated with attacking and eating a prey, disengaging from a prey item, and data on the acceptability of a specific prey type.

For each time step of one second, the movement parameters and co-ordinates are updated for each individual mite. Individuals that have a distance from the centre that is greater than or equal to the radius of the leaf are determined to be either on the stem or on the edge of the leaf. If on the edge of the leaf, the mite is set to bounce off the edge. The direction and speed of the bounce are determined by the original direction of the collision and a random variable. If the mite is on the area defined as the stem or the corridor between patches, the transit parameters allocate this mite to another leaf with a defined transition time. During transition no predation can occur. Once allocated to another patch, or having bounced off the patch edge, the model determines if a collision has undertaken with another mite. A collision occurs when the co-ordinates of the diameter of the mite overlap with another mite. If it has collided with a con-specific mite, the mites disengage. When a predator collides with a prey individual, the prey is consumed with a delay for handling

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time as described above. The time is then updated and the simulation continues if the time is less than the total simulation time, or otherwise ends.

This model is partially stochastic. Some variables, such as the direction of turning and speed for each individual predator or prey mite, are obtained with the aid of a random number generator. Other variables, such as the time for prey consumption, are deterministic.

Model parameters and simulations

The parameters of transit time between leaves, speed and the rate of turning were determined experimentally. Adult male *A. fallacis* were placed on a 3 cm diameter leaf patch on wet cotton wool, as above. These predators had been fed to satiation prior to the experiment. No prey were present on the experimental leaf patch for these trials. Prior to being used in the experiment they were left for at least one hour to acclimatize to their patch. For five minutes, the movement of an individual *A. fallacis* was recorded by tracing its paths on a transparent plastic sheet placed above the leaf patch. The traced paths allowed measurement of the mite walking distance and turning rate. A 'turn' was defined as a change in direction of more than 45°, after $\geq$ 3 mm of walking with less than a 45° change in direction (three millimeters is approximately three body lengths of an average adult *A. fallacis*). Turning rates were only estimated from observations in which a mite had moved more than 5 mm.

From these experiments, simulated mites were programmed as follows. Walking speed was set at 0.26 and 0.04 mm per second for predator and prey, respectively. Turning rates were set at 0.04 and 0.01 s^{-1}, for predator and prey respectively. The resulting movement by the simulated mites closely resembled that of the actual observations (Fig. 2). The radius of both predator and prey was set at 0.45mm. The time for both predator and prey mites to move between patches was determined by placing mites on two, connected leaves (as described above). The time to move from one leaf to another was from when a mite left the radius of one leaf and entered the radius of another. The resulting mean interpatch transit times used in the model were 173 or 510 s, for predator and prey respectively. The value of T_h used in all the simulations was *a priori* decided to be the value of T_h derived from the least-squares analysis of the preliminary data of functional response

of *A. fallacis* on *P. ulmi* from single patch experiments, and was set at 34 301 s (9 h 31 min). The width of the stem or corridor used in the simulations comparing experimental and simulation data was 1.0 mm in radius, which was approximately that of an actual apple leaf stem. The stem width (or measure of connectivity) varied from 0.05 – 4.00 mm in other simulations.

Results

The primary result from this study was that in *no* experimental or simulation trial did increasing patch number or connectivity change the functional response of *A. fallacis* from a type II to a type III. The value of L_1 (the coefficient of the linear term from the logistic regression equation, Equation 1) was always negative, and significantly less than 0 ($P<0.039$) in every case except one, always indicating the functional response to be of type II form (Juliano 2001) (Tables 1 & 2). The exception was for the simulated predator-prey interaction in the 4-patch system with a connectivity of 0.05 (Table 2), wherein L_1 was still negative and was still significantly less than 0 at the $P<0.10$ level, at $P=0.083$. The order of the approximating polynomial function used in equation 1, as selected by AIC_c, did not alter the sign of L_1: while a linear function was most commonly selected, if a quadratic or cubic polynomial was used instead, L_1 was still estimated as negative. In this sense our classification of all functional responses as type II is robust to model uncertainty. Note that the sizes of the L_1 values (Tables 1 & 2) are not all directly comparable, since for this type of data they typically increase with the order of the approximating polynomial function.

The simulation model approximated the functional response of live mites well (Fig. 3). Tests comparing experimentally and simulation derived attack rates (D_a) and handling time (D_{Th}) indicated no significant differences ($P \geq 0.08$) (Table 1). However, no such test was undertaken for the 1-patch system, as for this system the model produced what was clearly a type I functional response, wherein the predation rate increased linearly until a maximum of two prey were consumed per day (Fig. 3).

The influence of patch number on functional response parameters

In experiments with live mites, the attack rate (*a*) of *A. fallacis* on *P. ulmi* was clearly influenced by patch number. The experimentally derived attack rate of *A. fallacis* on a single patch decreased approximately five-fold to that observed on the six patch system (Table 1). Similar results were observed in the simulation data, both in tests comparing number of patches and in results examining patch connectivity below. The results for the high attack rates on 1-patch systems were apparent in the predicted prey mortality. At all prey densities (0.10, 0.50 and 1.00 arena^{-1}) the highest mortality predicted by the response curves was observed in a 1-patch system (Table 1). This predation rate also dropped from the 2-patch to 4-patch system, but the estimates from the 4-patch system were similar or only slightly higher than those observed in the 6-patch analysis. Thus the probability of even small numbers of prey being consumed is much higher where there are fewer patches.

In contrast to the attack rate, estimates of the handling time (T_h) stayed relatively similar across all experiments and simulation trials. Differences in the T_h estimates between trials are primarily due to the response curve not reaching a plateau, as most evident in the differences for T_h in the 6-patch arena with experimental and simulation data (Table 1). Further trials with high mite densities would likely have increased the accuracy of these estimates.

The influence of patch connectivity

The influence of patch connectivity on the functional response was examined using the simulation model. As previously stated, in these simulations the functional responses were of type II form, with L_1 being negative and significantly less than 0 for all trials (*P*<0.039). The only exception was the trial with four patches and a connectivity of 0.05 (Table 2), wherein L_1 was still negative and was still significantly less than 0 at the *P*<0.10 level, at *P*=0.083. The resulting functional responses always being of type II form was surprising, as we had suspected a type III response would be likely in simulations such as with the 6-patch system and the lowest connectivity treatment of 0.05mm. This degree of connectivity was 80 times lower than in the 4.00mm treatment and correspondingly the simulated predator was observed to move between the treatments much less frequently.

Similar to the previous results, increasing the number of patches decreased the attack rate (a) in all simulations, though the changes from that observed for a in the 2-patch to 4-patch system was much greater than for the difference between the 4-patch and 6-patch systems. To test if such differences in a were significant, we statistically compared the estimate of a in the 2- and 6-patch systems with 0.25 mm connectivity. Estimates of D_a for this analysis confirmed a were significantly higher in the 2-patch system ($D_a = -1.49 \pm 0.62$; $P = 0.02$). From these simulation and experimental results, it would appear that the decrease in a approximates a negative exponential response with increasing patch number (Tables 1, 2). In accordance with the decreased attack rate, the predicted predation rates were lowest in the 6-patch system. In the 2-patch system with high connectivity nearly all available prey are predicted to have been killed at high connectivity, even at low prey densities. In contrast in the 6-patch system only approximately half the available prey were killed even in systems with high connectivity (Table 2).

Increasing the connectivity increased the attack rate in all simulations with two, four or six patches (Table 2, Fig. 4). A four-fold increase in connectivity resulted in an approximate doubling of a for each system. For example, we observed a significantly higher value of a for the 4.00mm connectivity than in the 0.05mm connectivity treatments of the 4-patch system ($D_a = 3.12 \pm 1.26$; $P = 0.02$) [all 66 possible pairwise analyses of treatments in this dataset were not analysed due to the risk of increased experiment-wise error rates, as well as being considered unnecessary]. Predicted mortality again increased in a non-linear fashion with increasing connectivity within each system of multiple patches (Table 2).

Slight differences observed in the handling time (T_h) for the simulated predator were not considered relevant here, as we programmed the predator with a constant handling time of 34 301 s (9 h 31 min). Observed slight differences in estimates between simulations again reflected the response curve not entirely reaching a plateau, as described in the previous section.

Discussion

The logical consequence of dispersal behavior is that the functional response will take on the type III form (Murdoch and Oaten 1975; Hassell et al. 1977; Hassell 1980). In our work, modifying dispersal rates by changing connectivity and patch number significantly changed the attack rate but did not alter the functional response type from a type II curve. These results were observed for both the experiments and simulations wherein predator-prey encounter rates were reduced to extremely low levels. As discussed in the introduction, several models and experimental studies have shown the type II response to be destabilizing and not to allow long-term population persistence, while type III responses have been found to be demographically stabilizing (Hassell and May 1973; Murdoch and Oaten 1975; Hassell and Comins 1978; Nunney 1980; Pech et al. 1992). In the light of these conclusions, the results from our study leads to at least two central questions: (i) have we realistically estimated the functional response type, and (ii) if the functional response of these predators is of type II form, how do predator-prey populations persist in nature?

There are several other studies that have indicated phytoseiid predators to have a type II functional response (e.g. Everleigh and Chant 1982; Lester and Harmsen 2002), and indeed no published studies have statistically demonstrated phytoseiids to have any other functional response type. Neither, however, have other workers looked at the functional response of these predators in a multi-patch framework. We feel that our experiments and simulation model more accurately reflect the functional response of these predators. Ideally, for the most accurate estimation, the functional response should be estimated in the field under natural conditions (e.g. Schenk and Bacher 2002). However, such an analysis with very small predators such as mites would be almost impossible. We feel that our experiments and simulations with multiple patches or leaves, between which a phytoseiid predator would have to move in order to obtain prey, is a realistic representation of the natural predator-prey interaction. We are thus confident that the functional response of these male predators to protonymphs and deutonymphs *P. ulmi* is indeed of type II form.

We chose this predator and prey combination specifically in an attempt to reduce variation within and between predators and available prey. Changes in the oviposition rate

over the duration of an adult female predator's life can influence feeding (e.g. Kishimoto and Takafuji 1997). Similarly, many studies have been undertaken with adult female prey, but these also lay eggs that may or may not be suitable prey for phytoseiids and can influence their functional response (Lester & Harmsen 2002). This study is the first to assess the functional response of male phytoseiids, but more importantly we wanted to focus specifically on the response of a predator to changes in patch number and connectivity without such noise. Further questions of how the predation-prey interaction changes with varying time to successfully move between patches, changes in patch size, and with different stages of prey, will be investigated in an additional paper.

Type II functional responses have been observed for a range of other predators in natural environments including lynx and fox (e.g. O'Donoghue et al. 1998; Angerbjörn et al. 1999). The question then arises of how predator and prey populations persist in such a relationship, when type II functional responses have been suggested as demographically destabilizing (Hassell and May 1973; Murdoch and Oaten 1975; Hassell and Comins 1978; Nunney 1980; Pech et al. 1992)? In contrast to these aforementioned studies, recent work by Williams and Martinez (2004) indicates that a slight modification to a type II functional response can stabilize food-web demographics and allow for long-term persistence. Their functional response is of intermediate form between that of a type II and III, with a lower attack rate (Williams and Martinez 2004). In orchard food webs a range of alternative prey items are attacked by phytoseiid predators (Woolhouse and Harmsen 1984; Wei and Walde 1997; Lester et al. 1998). As a result of such alternative prey, phytoseiid attack rates on *P. ulmi* can be lowered but still appear to be of the type II form (Lester and Harmsen 2002). Perhaps the intermediate functional response as described by Williams and Martinez (2004) is occurring for *A. fallacis* and *P. ulmi* in our orchard systems. However, statistical methods are not currently available for the determination of these intermediate functional response types and more work in this area is required (Williams and Martinez 2004).

Another mechanism for the persistence of these predator-prey interactions with a type II functional response may be that these species conform to metapopulation dynamics. Under metapopulation dynamics, local extinction on patches or even entire plants may not be of relevance as recolonization events lead to community persistence. Two key references

lead us to suspect that this is the case for phytoseiid predators. Firstly, Nachman (1991) demonstrated that predator-prey communities exhibited unstable dynamics at the level of individual plants, but persistence at the regional scale was maintained through a shifting mosaic of interactions. Secondly, Walde (1994) found that while the phytoseiid predator *T. pyri* on isolated trees appeared to have a high probability of driving *P. ulmi* populations to extinction, the probability of predator and prey population persistence was increased in larger groups of trees. Other studies also lend support to the concept that these populations assume stochastic metapopulation dynamics (McCauley et al. 2000; Nachman 2001), implying that phytoseiids could exhibit a type II functional response but metapopulation dynamics would allow predator-prey persistence.

The effects of increased predator dispersal resulting in higher predation rates and decreasing prey densities have been observed elsewhere (Nachman 1987, Reeve 1988, Holyoak and Lawler 1996). Such a result must decrease the duration of predator-prey persistence in individual patches. However, unless alternative prey or dispersal does result in a change to the modified type II functional response as described by Williams and Martinez (2004), factors such as metapopulation dynamics seem likely to account for long-term population persistence in orchard ecosystems. Just which scenario is correct is of high importance for the management of predators with type II functional responses, as each has vastly different implications. In order to enhance populations of phtyoseiid predators, or conserve lynx, should we maintain metapopulation structure or encourage alternative prey species?

Acknowledgements

References

Angerbjörn, A., Tannerfeldt, M., and Erlinge, S. 1999. Predator-prey relationships: arctic foxes and lemmings. J. Anim. Ecol. **68**: 34-49.

Blackwood, J.S., Schausberger, P., and Croft, B.A. 2001. Prey-stage preference in generalist and specialist phytoseiid mites (Acari: Phytoseiidae) when offered *Tetranychus urticae* (Acari: Tetranychidae) eggs and larvae. Environ. Entomol. **30**: 1103-1111.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, N.Y.

Croft, B.A., and Blyth, E.J. 1979. Aspects of the functional, ovipositional and starvation response of *Amblyseius fallacis* to prey density. *In* Recent Advances in Acarology, Volume I. *Edited by* J.G. Rodriguez. Academic Press, N.Y. pp. 41-47.

Everleigh, E.S., and Chant, D.A. 1982. Experimental studies on acarine predator-prey interactions: the effects of predator density on prey consumption, predator searching time, and the functional response to prey density (Acarina: Phytoseiidae). Can. J. Zool. **60**: 611-629.

Hassell, M.P. 1980. Foraging strategies, population models and biological control: a case study. J. Anim. Ecol. **49**: 603-628.

Hassell, M.P., and Comins, H.N. 1978. Sigmoid functional responses and population stability. Theor. Popul. Biol. **14**: 62-67.

Hassell, M.P., and May, R.M. 1973. Stability in insect host-parasite models. J. Anim. Ecol. **42**: 693-726.

Hassell, M.P., Lawton, J.H., and Beddington, J.R. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. **46**: 249-262.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitisim. Can. Entomol. **91**: 385-398.

Holyoak, M., and Lawler, S.P. 1996. The role of dispersal in predator-prey metapopulation dynamics. J. Anim. Ecol. **65**: 640-652.

Juliano, S.A. 2001. Nonlinear curve fitting: predation and functional response curves. *In* Design and analysis of ecological experiments. 2nd ed. *Edited by* S.M. Scheiner and J. Gurevitch. Oxford University Press, N.Y. pp. 178-196.

Kishimoto, H., and Takafuji, A. 1997. Variations in the life-history parameters among populations of *Amblyseius womersleyi* Schicha with different diapause characteristics (Acari: Phytoseiidae). Appl. Entomol. Zool. 32: 395-401.

Lester, P.J., and Harmsen, R. 2002. Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. J. Appl. Ecol. **39**: 455-468.

Lester, P.J., Thistlewood, H.M.A., and Harmsen, R. 1998. The effects of refuge size and number on acarine predator-prey dynamics in a pesticide-disturbed apple orchard. J. Appl. Ecol. **35**: 323-331.

Lester, P.J., Pree, D.J., Thistlewood, H.M.A., Trevisan, L.M., and Harmsen, R. 1999. Pyrethroid encapsulation for conservation of acarine predators and reduced spider mite (Acari: Tetranychidae) outbreaks in apple orchards. Environ. Entomol. **28**: 72-80.

Lester, P.J., Thistlewood, H.M.A., and Harmsen, R. 2000. Some effects of pre-release host-plant on the biological control of *Panonychus ulmi* by the predatory mite *Amblyseius fallacis*. Exp. Appl. Acarol. **24**: 19-33.

Lord, F.T. 1972. Comparisons of the abundance of the species composing the foliage inhabiting fauna of apple trees. Can. Entomol. **104**: 731-749.

McCauley, E., Kendall, B.E., Janssen, A., Wood, S., Murdoch, W.W., Hosseini, P., Briggs, C.J., Ellner, S.P., Nisbet, R.M., Sabelis, M.W., and Turchin, P. 2000. Inferring colonization processes from population dynamics in spatially structured predator-prey systems. Ecology **81**: 3350-3361.

Murdoch, W.W., and Oaten, A. 1975. Predation and population stability. Adv. Ecol. Res. **9**: 1-131.

Nachman, G. 1987. Systems analysis of acarine predator-prey interactions. II. The role of spatial processes in system stability. J. Anim. Ecol. **56**: 267-281.

Nachman, G. 1991. An acarine predator–prey metapopulation system inhabitating greenhouse cucumbers. Biol. J. Linn. Soc. **42**: 285–303.

Nachman, G. 2001. Predator-prey interactions in a nonequilibrium context: the metapopulation approach to modeling "hide-and-seek" dynamics in a spatially explicit tri-trophic system. Oikos 94: 72-88.

Nunney, L. 1980. The influence of the type 3 (sigmoid) functional response upon the stability of predator-prey difference models. Theor. Popul. Biol. **18**: 257-278.

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., and Hofer, E.J. 1998. Functional responses of coyotes and lynx to the snowshow hare cycle. Ecology **79**: 1193-1208.

Oatman, E.R. 1973. An ecological study of arthropod populations on apple in northeastern Wisconsin: population dynamics of mite species on the foliage. Ann. Entomol. Soc. Am. **66**: 122-131.

Parent, B. 1967. Population studies of phytophagous mites and predators on apple in southwestern Quebec. Can. Entomol. **99**: 771-778.

Pech, R.P., Sinclair, A.R.E., Newsome, A.E., and Catling, P.C. 1992. Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. Oecologia **89**: 102-112.

Reeve, J.D. 1988. Environmental variability, migration, and persistence in host-parasitoid systems. Am. Nat. **132**: 810-836.

Rogers, D. 1972. Random search and insect population models. J. Anim. Ecol. **41**: 369-383.

SAS. 1999. The SAS system for Windows, version 8.02. SAS Institute, Cary, North Carolina, USA.

Schenk, D., and Bacher, S. 2002. Functional response of a generalist insect predator to one of its prey species in the field. J. Anim. Ecol. **71**: 524-531.

Walde, S.J. 1994. Immigration and the dynamics of a predator-prey interaction in biological-control. J. Anim. Ecol. **63**: 337-346.

Wei, Q.C., and Walde, S.J. 1997. The functional response of *Typhlodromus pyri* to its prey, *Panonychus ulmi*: the effect of pollen. Exp. Appl. Acarol. **21**: 677-684.

Williams, R.J., and Martinez, N.D. 2004. Stabilization of chaotic and non-permanent food-web dynamics. Eur. Phys. J. B **38**: 297-303.

Woolhouse, M.E.J., and Harmsen, R. 1984. The mite complex on the foliage of a pesticide-free apple orchard: population dynamics and habitat associations. Proc. Entomol. Soc. Ont. **115**: 1-11.

Table 1. Functional response parameters from experiments with *A. fallacis* feeding on *P. ulmi*, and from computer simulations of this interaction on one to six leaf patches. L_1 values are coefficients from the logistic regression assessing the type of response; all values are significantly negative indicating a type II response. Significance tests examine if the coefficient is significantly different from 0: ns= not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. D_a and D_{th} represent analyses comparing results from experimental and simulation data, for differences in *a* or T_h respectively. Values shown are estimates ± standard errors; *n*= 4 for both experiments and simulations.

Number of patches per arena	L_1	*a* (prey attack h^{-1})	T_h (h^{-1})	Predicted mortality at prey density (prey arena^{-1}):		
				0.10	0.50	1.00
One patch						
Experiments	-0.15 ± 0.04***	1.62 ± 1.10 ns	0.36 ± 0.08***	0.08	0.36	0.64
Simulations	β	β	β	0.10	0.50	1.00
D_a or D_{Th}		β	β			
Two patch						
Experiments	-0.10 ± 0.03***	0.96 ± 0.42*	0.40 ± 0.07***	0.06	0.28	0.50
Simulations	-0.42 ± 0.15**	3.71 ± 1.43*	0.48 ± 0.03***	0.10	0.43	0.74
D_a or D_{Th}		2.75 ± 2.30 ns	0.08 ± 0.08 ns			
Four patch						
Experiments	-0.04 ± 0.01**	0.32 ± 0.13*	0.39 ± 0.07***	0.03	0.13	0.25
Simulations	-0.06 ± 0.01***	1.09 ± 0.32**	0.45 ± 0.03***	0.06	0.29	0.52
D_a or D_{Th}		0.77 ± 0.43 ns	0.06 ± 0.08 ns			
Six patch						
Experiments	-0.04 ± 0.02*	0.35 ± 0.16*	0.27 ± 0.08**	0.03	0.14	0.28
Simulations	-0.06 ± 0.02***	0.67 ± 0.21**	0.42 ± 0.05***	0.05	0.22	0.41
D_a or D_{Th}		0.31 ± 0.36 ns	0.15 ± 0.10 ns			

β The simulation data for a one patch system clearly corresponded to a type I functional response, so was not analysed here.

Table 2. Functional response parameters L_1, a and T_h, from simulations. The number of patches was varied between simulations, as well as the connectivity which was modified by varying the diameter of the corridor connecting patches. Patch diameter = 30mm. Significance tests examine if the coefficient is significantly different from 0: ns= not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Values shown are estimates $\pm$ standard errors; n= 6 simulations.

Patch connectivity (mm)	L_1	a (prey attack h^{-1})	T_h (h^{-1})	Predicted mortality at prey density (prey arena^{-1}):		
				0.10	0.50	1.00
Two patch						
0.05	-0.13 ± 0.03***	1.28 ± 0.38**	0.39 ± 0.05***	0.07	0.32	0.57
0.25	-0.16 ± 0.03***	2.01 ± 0.57**	0.41 ± 0.04***	0.08	0.38	0.67
1.00	-0.42 ± 0.15**	3.71 ± 1.43*	0.48 ± 0.03***	0.10	0.43	0.74
4.00	-4.81 ± 2.16*	46.69 ± 39.61 ns $^\beta$	0.49 ± 0.01***	0.10	0.49	0.85
Four patch						
0.05	-0.04 ± 0.02 ns	0.32 ± 0.08***	0.29 ± 0.07***	0.03	0.13	0.25
0.25	-0.08 ± 0.02***	0.67 ± 0.16***	0.39 ± 0.05***	0.05	0.22	0.41
1.00	-0.06 ± 0.01***	1.09 ± 0.32**	0.45 ± 0.03***	0.06	0.29	0.52
4.00	-0.40 ± 0.11***	3.44 ± 0.87***	0.47 ± 0.02***	0.09	0.43	0.73
Six patch						
0.05	-0.04 ± 0.02*	0.25 ± 0.06***	0.33 ± 0.06***	0.02	0.11	0.21
0.25	-0.06 ± 0.02***	0.53 ± 0.14***	0.41 ± 0.04***	0.04	0.19	0.35
1.00	-0.06 ± 0.02***	0.67 ± 0.21**	0.42 ± 0.05***	0.05	0.22	0.41
4.00	-0.19 ± 0.06**	1.41 ± 0.26***	0.45 ± 0.02***	0.07	0.33	0.58

$^\beta$ We were unable to obtain model convergence to the two patch, 4mm stem width, simulation data. The data appeared to better approximate a type I functional response.

Fig. 1. A flow diagram representing our simulation model of mite predator and prey interactions on leaf disks of varying connectivity.
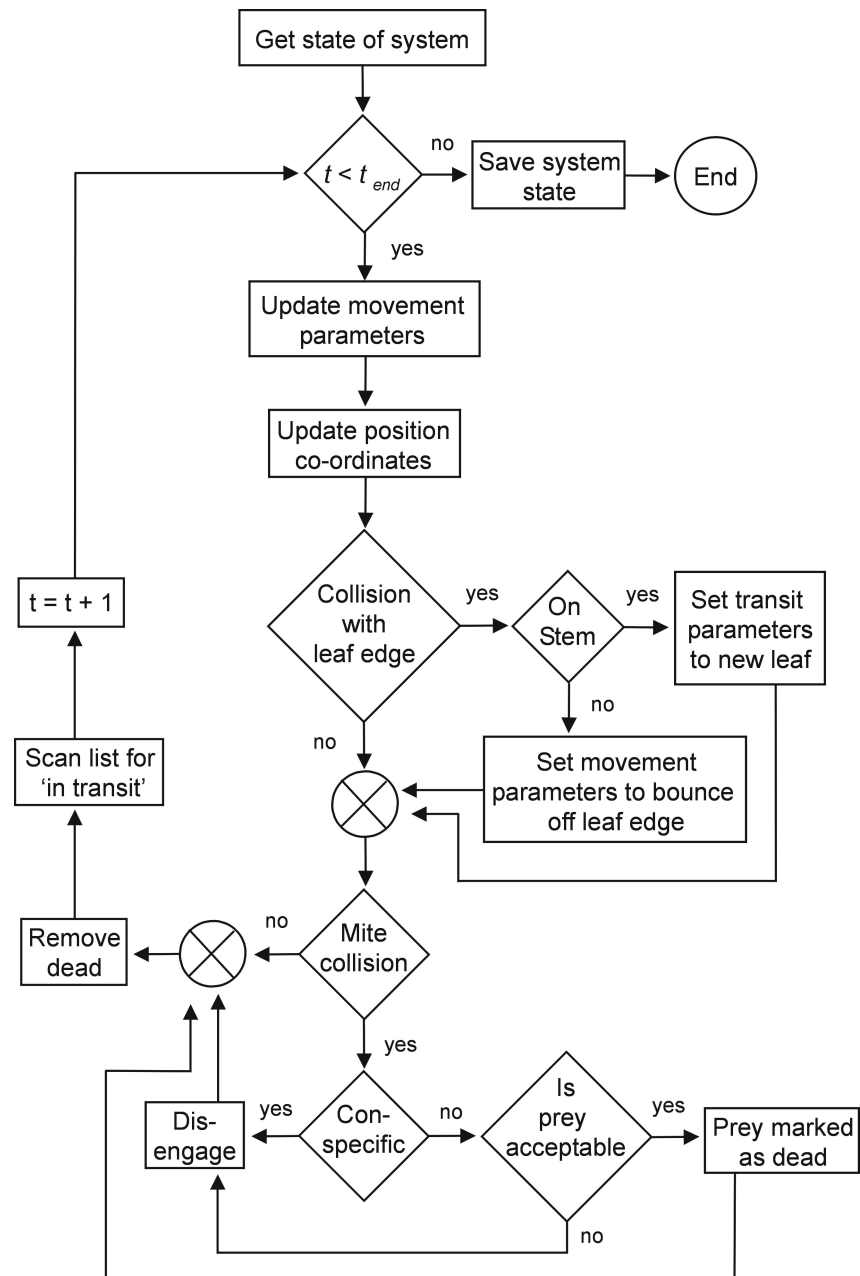
Fig. 2. Traces of mite movement on an individual patch. The bottom two graphs for each species show actual traces of the movement of both predator and prey. These traces were taken to gain information on mite speed and turning rates. The top two graphs for both *A. fallacis* and *P. ulmi* show results from simulations. For *A. fallacis*, the movement recordings are for 5 min intervals, while a 10 min interval was used for *P. ulmi*. The circles indicate the leaf-disk border.
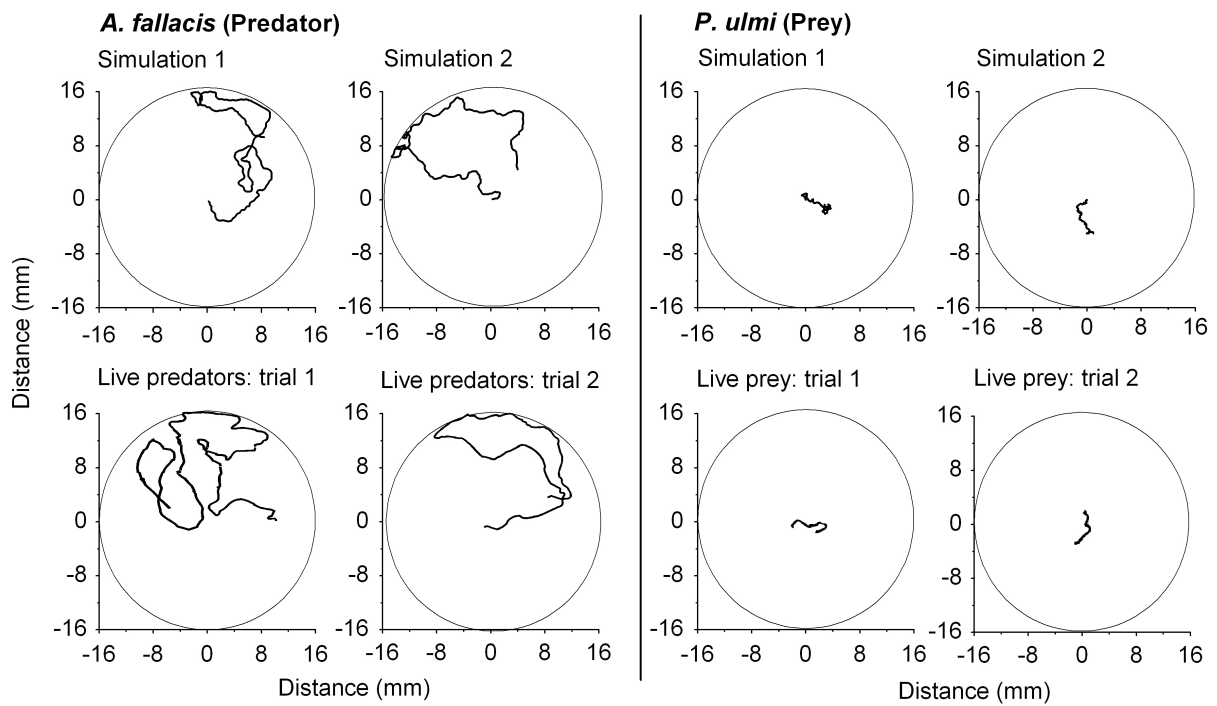
Fig. 3. The functional responses of *A. fallacis* attacking *P. ulmi* on one, two, four or six interconnected leaf systems. D_a and D_{Th} are results from analyses testing for differences between the attack rates (*a*) and the handling times (*Th*) of experimental and simulated data ± standard errors; ns= no significant difference. Fitted lines are from the functional response equations, with the exception of the one-leaf simulated data, which was obviously a type I. No analysis comparing *a* and T_h were thus carried out for the one-leaf system. *n*= 4; error bars = 1 standard error. (□ ----), data from experiments; (■ —), data from simulations. Overlying points are offset slightly.
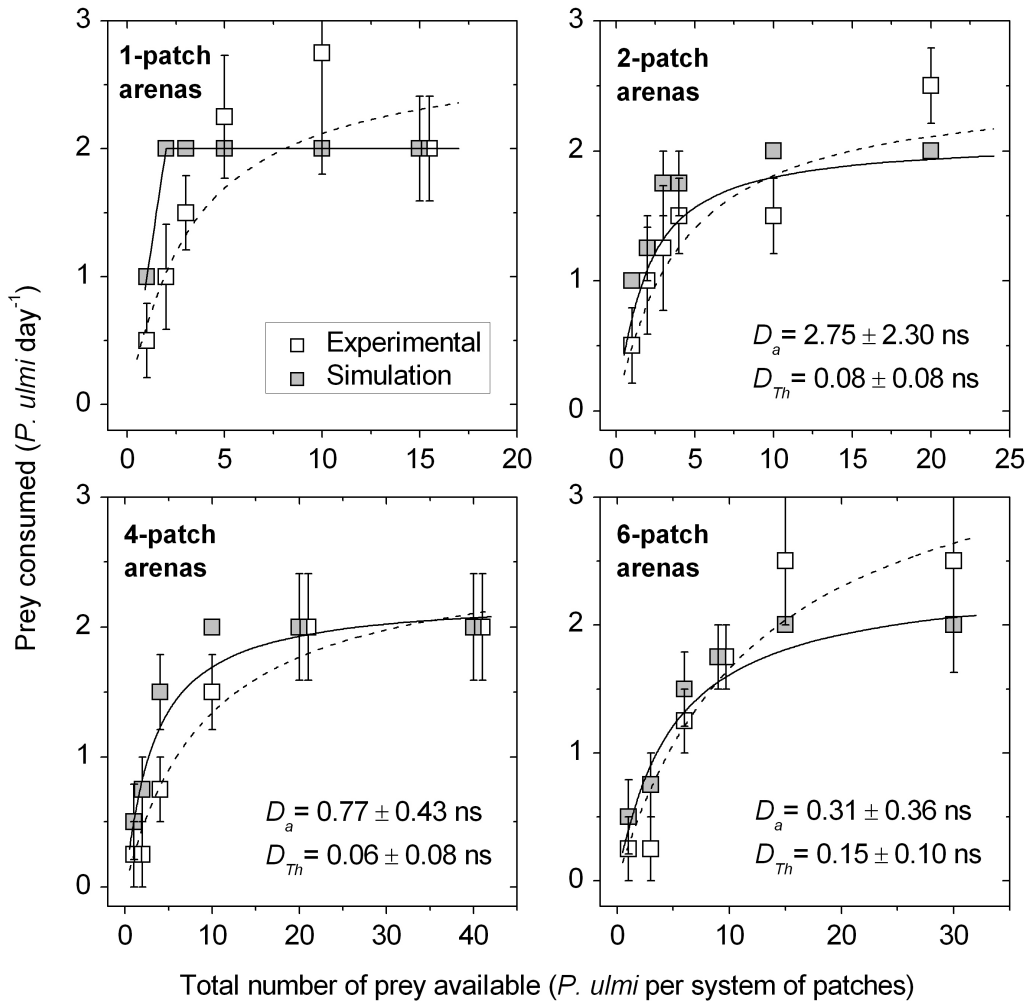
Fig. 4. Simulations of the functional response of predators on a two, four or six patch system. The different lines on each graph represent simulations where the corridor between patches was increased from a radius of 0.05 mm to 4.00mm; thus changing the likelihood of a predator (or prey) to move between patches. The parameters *a* represent attack rates (prey day^{-1}) in the different simulations. The attack rate for 4.00mm in the 2-patch arena (ψ) was unable to be accurately estimated due to a lack of convergence.