

Does altering patch number and connectivity change the predatory functional response type? Experiments and simulations in an acarine predator–prey system

P.J. Lester, J.M. Yee, S. Yee, J. Haywood, H.M.A. Thistlewood, and R. Harmsen

Abstract: In multipatch landscapes, understanding the role of patch number and connectivity is key for the conservation of species under processes such as predation. The functional response is the most basic form of the predator–prey interaction. Two common response types exist: a decelerating curvilinear increase in prey consumption with prey density to a plateau (type II) and a sigmoidal-shaped curve (type III). Type II responses have been observed for a variety of predators, though only type III responses allow long-term persistence and are demographically stabilizing. We tested the hypothesis that the functional response type can change from a type II to a type III with increasing patch number and (or) decreasing connectivity. The predatory mite *Amblyseius fallacis* (Garman, 1948) has previously been shown to have a type II response when feeding on *Panonychus ulmi* (Koch, 1839). We examined this predator–prey interaction using experiments that varied in patch number, and simulations that varied in both patch number and connectivity. In no experimental or simulation trial did altering patch number or connectivity change the predator’s functional response from type II to type III, even with an 80-fold decrease in patch connectivity. How do predators with this demographically destabilizing functional response persist? Hypotheses regarding metapopulations and alternative prey are discussed.

Résumé : Dans les paysages composés de multiples parcelles, la compréhension du rôle du nombre de parcelles et de leur connectivité est essentielle pour la conservation des espèces qui subissent des processus tels que la prédation. La réponse fonctionnelle est la forme la plus élémentaire de l’interaction prédateur–proie. Il existe deux types communs de réponses fonctionnelles, une augmentation curviligne en décélération de la consommation des proies en fonction de la densité des proies jusqu’à l’atteinte d’un plateau (type II) et une courbe de forme sigmoïde (type III). Des réponses de type II s’observent chez une variété de prédateurs, bien que seules les réponses de type III permettent une permanence à long terme et génèrent un équilibre démographique. Nous éprouvons l’hypothèse qui veut le type de réponse fonctionnelle puisse changer du type II au type III lorsque le nombre de parcelles augmente et (ou) lorsque la connectivité diminue. Il est connu que l’acarien prédateur *Amblyseius fallacis* (Garman, 1948) possède une réponse fonctionnelle de type II lorsqu’il se nourrit de *Panonychus ulmi* (Koch, 1839). Nous étudions cette relation prédateur–proie à l’aide d’expériences qui font varier le nombre de parcelles et à l’aide de simulations qui font varier à la fois le nombre de parcelles et la connectivité. Dans aucune des expériences et des simulations, le changement du nombre de parcelles ou de la connectivité ne transforme la réponse fonctionnelle de type II en type III, même lorsque la connectivité des parcelles est réduite de 80 fois. Comment les prédateurs réussissent-ils à se maintenir malgré cette réponse fonctionnelle à effet potentiel déstabilisateur sur la population? Nous présentons certaines hypothèses impliquant les métapopulations et les proies de rechange.

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Introduction

The relationship between prey density and a predator's consumption rate is known as the functional response (Solomon 1949). Theory holds that there are three main types of functional response: a linear rise in prey consumption with increasing prey density to a plateau (type I), a decelerating curvilinear rise to a plateau (type II), and a sigmoidal shaped curve to a plateau (type III) (Holling 1959). Type I functional responses have been suggested as exclusive to filter feeders (Jeschke et al. 2004). Type II and III functional responses have been generally considered the norm for non-filter feeders, with the type II being the most frequently observed (Begon et al. 1996). The functional response of a wide variety of predators has been suggested to be of type II form, including flatworms (Beier et al. 2004), insects (Aukema and Raffa 2004), predatory mites (Lester and Harmsen 2002), owls (Tome 2003), lynx (O'Donoghue et al. 1998), and even whales (Mackinson et al. 2003). Despite the relatively widespread nature of the type II response 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 shown to be demographically stabilizing (Hassell and May 1973; Murdoch and Oaten 1975; Hassell and Comins 1978; Nunney 1980; Pech et al. 1992). Factors thought responsible for the generation of type III functional responses include prey switching, or whenever an increase in prey density leads to an increase in the predators' searching efficiency or a decrease in handling time (Begon et al. 1996).

For many of the predators cited above as having a type II response, their prey are known to occur in distinct and sometimes widely separated patches that the predators must move between. Such enforced predator dispersion is generally not incorporated into experiments examining the functional response, which are often undertaken within single-patch systems (e.g., Lester and Harmsen 2002). Studies at a larger scale of multiple patches, although more difficult and complex, may lead to different results. The logical consequence of such dispersal behaviour is that the functional response will take on the type III form (Murdoch and Oaten 1975; Hassell et al. 1977; Hassell 1980). In this paper we test this hypothesis that functional response of a predator will change from type II to type III as a result of increasing patch number and (or) decreasing connectivity.

As a model system, we examined the functional response of the acarine predator *Amblyseius fallacis* (Garman, 1948) feeding on *Panonychus ulmi* (Koch, 1839). Previous studies have shown 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, the difficulty in following small predators such as mites has led these authors to assess the functional response on single, isolated patches. For mites these patches are often small leaf disks, confining predator and prey movement to a few square centimetres. A system containing a set of patches with varying connectivity would more closely represent the natural environment of these mites 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 such predator and prey species. For example, 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), and this could perhaps be considered evidence for the existence of a type III functional response.

Materials and methods

Predator and prey mite colonies

Panonychus ulmi were reared on seedlings of apple (*Malus domestica* (Borkh.) Borkh.) and peach (*Prunus persica* (L.) Batsch), maintained at 24 ± 2 °C and 60% RH and in continuous light. A 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 4 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 ± 1 °C, 60% RH, and 16 h light (L) : 8 h dark (D) photoperiod. Three times weekly, leaves of the kidney bean, *Phaseolus vulgaris* L., infested with the prey *Tetranychus urticae* Koch, 1836, were added to each rearing unit. The *T. urticae* colony was reared on bean plants at 24 ± 1 °C, 60% RH, and 16 h L : 8 h D. Apple leaves with *P. ulmi* were also added approximately once per 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. These two prey stages are of similar size and were considered one prey 'type' for the statistical analysis. Tests were undertaken on 3 cm diameter (total surface area = 7.1 cm²) *M. domestica* '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 the mites to these leaves. We examined the functional response on a single leaf patch, or on two, four, or six interconnected leaf patches. To connect the leaf patches, leaves were cut so that they retained 2.0 cm of stem length. 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 one predator and *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 1 day after 2 consecutive days of preconditioning of predator mites to the leaf, prey stage, and prey density.

The functional response type of the predators was determined following the methods of Juliano (2001), using a

polynomial of selected order to determine the functional response shape and then estimating a relevant functional response model by nonlinear least squares. 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 is the number of prey eaten, N_0 is the initial number of prey available, and thus N_e/N_0 is the probability that a prey is eaten. That probability, using for illustration the most general polynomial function considered, was modelled as

$$[1] \frac{N_e}{N_0} = \frac{\exp(L_0 + L_1N_0 + L_2N_0^2 + L_3N_0^3 + L_4N_0^4)}{1 + \exp(L_0 + L_1N_0 + L_2N_0^2 + L_3N_0^3 + L_4N_0^4)}$$

Maximum-likelihood estimates of parameters L_0 up to L_4 (as required) were obtained using PROC CATMOD in SAS[®] (SAS Institute Inc. 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 eq. 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):

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

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 that 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):

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

Iterative application of the Gauss-Newton method in PROC NLIN (SAS Institute Inc. 1999) was used to estimate the parameters in eqs. 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:

$$[4] 0 = N_0 - N_0 \exp\{[a + jD_a][(T_h + jDT_h)N_e - T]\} - N_e$$

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 DT_h estimate the respective differences in the values of the parameters a and T_h , between the populations (Juliano 2001). D_a and DT_h values were considered statistically significant at $P < 0.05$, which would indicate a significantly different attack rate or prey handling time, respectively.

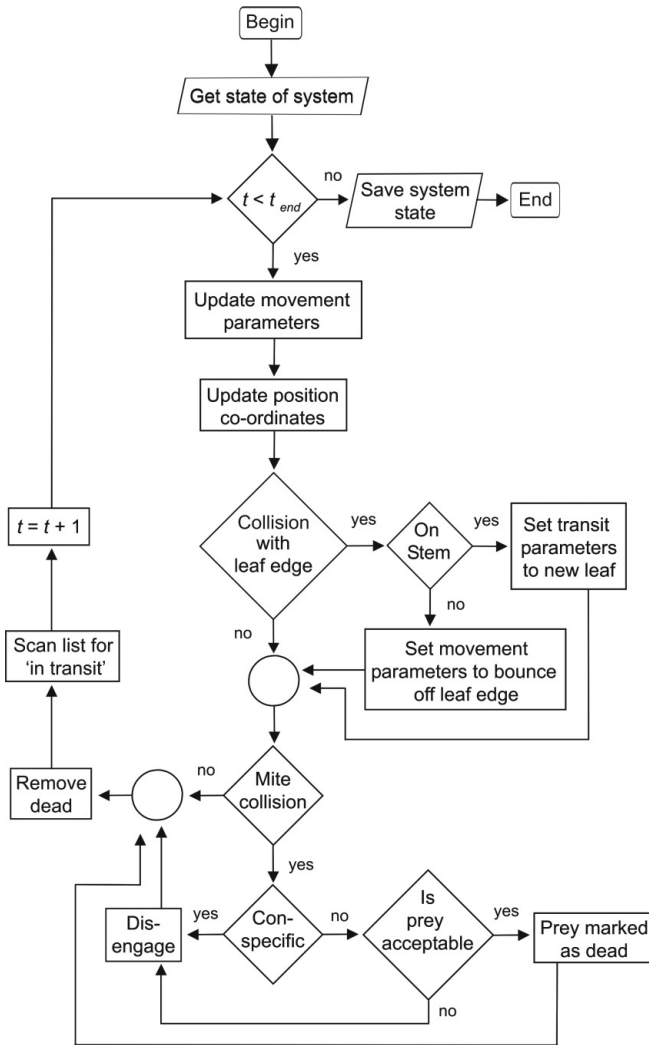
Overview of the predator-prey simulation model

Using a computer model we were able to simulate the above experimental work (i.e., systems of single or multiple interconnected leaves, with one predator and prey densities of 0.17–40 *P. ulmi* per leaf), but also alter the relative connectivity between patches. The model designed for this study was an individual, list-based model (Fig. 1). For input, individual files were 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 walked 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 high (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 1 s, 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 conspecific mite, the mites disengage (note that here, only prey can be conspecific as there

Fig. 1. A flow diagram representing our simulation model of predator and prey interactions on leaf disks of varying connectivity. Flow diagram graphics: rounded rectangle, terminals of the algorithm; rectangle, calculation procedure or function; diamond, logical decision or branch point; slanted parallelogram, input or output; circle, connector joining multiple algorithm paths; arrow graphics, flow of algorithm steps.



was only one predator per arena). When a predator collides with a prey individual, the prey is consumed with a delay for handling 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, were 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 empirically. 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 ex-

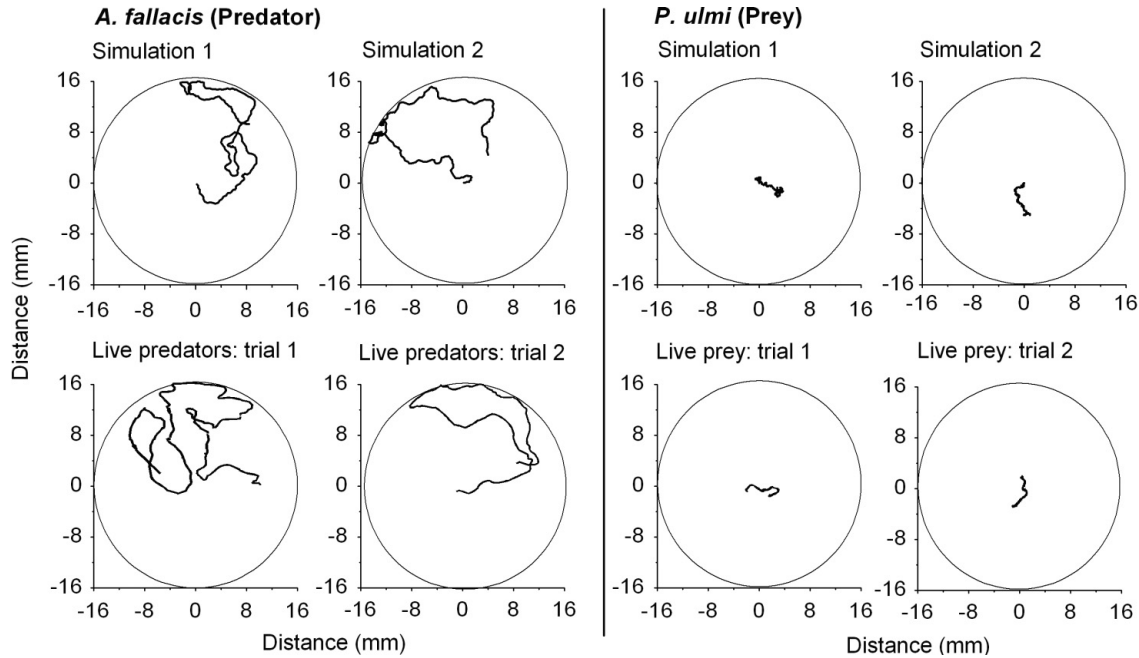
perimental leaf patch for these trials. Prior to being used in the experiment they were left for at least 1 h to acclimatize to their patch. The movement of an individual mite was recorded by tracing its paths on a transparent plastic sheet placed above the leaf patch. For *A. fallacis* the movement recordings are for 5-min intervals, while a 10-min interval was used for *P. ulmi*. The traced paths allowed measurement of the mite walking distance and turning rate. For the purpose of estimating turning behaviour, the walking paths were approximated by a series of connected line segments and the turn parameters were estimated from the line segments. A "turn" was defined as a change in direction of more than 45° following ≥3 mm of walking without any change in direction (3 mm is approximately three body lengths of an average adult *P. ulmi* or *A. fallacis*). Turning rates (expressed as turns per second) 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·s⁻¹ for predator and prey, respectively. Maximum turning rates were set at 0.04 and 0.01 turn·s⁻¹, corresponding to one turn every 25 and 100 s, for predator and prey respectively. The elapsed time between successive turn events was selected from a uniform distribution ranging from 0 to 25 s and 0 to 100 s for the predator and prey, respectively. The simulated turning angle at a turn event was randomly selected from a uniform distribution ranging from -90° to +90°. Selecting the elapsed time between turn events and the turn angle from uniform distributions serves to simulate a smooth walking path. 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 0.45 mm. The time for both predator and prey mites to move among 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 and 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 to 4.00 mm in other simulations. Simulations only ever had one predator per simulated arena, but prey densities ranged from 1 to 40 prey per simulated arena of one to six patches.

Results

The primary result from this study was that in no experimental or simulation trial did increasing patch number or decreasing 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, eq. 1) was always negative and significantly less than 0 ($P < 0.039$) in every case except one, always indicat-

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 *Amblyseius fallacis* and *Panonychus 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.



ing 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 four-patch system with a connectivity of 0.05 (Table 2), wherein L_1 was still negative but with $P = 0.083$. The order of the approximating polynomial function used in eq. 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 and 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 (DT_h) indicated no significant differences ($P \geq 0.08$) (Table 1). However, no such test was undertaken for the one-patch system, as for this system the simulation produced what appeared to be a type I functional response, wherein the predation rate increased linearly until a maximum of two prey were consumed per day (Fig. 3a). A type II functional response was unable to be fitted to this data because of the lack of convergence for model parameters in the nonlinear least squares estimation.

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 was approximately five times 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 one-patch systems were apparent in the predicted prey mortality. At the prey densities (0.10, 0.50, and 1.00 prey-arena⁻¹) the highest mortality predicted by the response curves was observed in a one-patch system (Table 2). This predation rate also dropped from the two- to four-patch system, but the estimates from the four-patch system were similar or only slightly higher than those observed in the six-patch analysis. Thus the probability of 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 six-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 but one ($P < 0.039$) (Table 2, Fig. 4b).

Similar to the previous results, increasing the number of patches decreased the attack rate (a) in all simulations, though the change from that observed for a in the two- to four-patch system was much greater than for the difference

Table 1. Functional response parameters from experiments with *Amblyseius fallacis* feeding on *Panonychus ulmi*, and from computer simulations of this interaction on one to six leaf patches.

	L_1	a (prey attacks·d ⁻¹)	T_h (d ⁻¹)	Predicted mortality at the following prey densities (prey·arena ⁻¹)		
				0.10	0.50	1.00
One patch per arena						
Experiments	-0.15±0.04***	1.62±1.10 ns	0.36±0.08***	0.08	0.36	0.64
Simulations	— [†]	— [†]	— [†]	0.10	0.50	1.00
D_a or DT_h	— [†]	— [†]	— [†]			
Two patches per arena						
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 DT_h		2.75±2.30 ns	0.08±0.08 ns			
Four patches per arena						
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 DT_h		0.77±0.43 ns	0.06±0.08 ns			
Six patches per arena						
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 DT_h		0.31±0.36 ns	0.15±0.10 ns			

Note: 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 DT_h represent analyses comparing results from experimental and simulation data for differences in a or T_h , respectively. Values are estimates ± SE; $n = 4$ for both experiments and simulations.

[†]The simulation data for a one-patch system appeared to correspond to a type I functional response, so was not analysed here.

Table 2. Functional response parameters L_1 , a , and T_h , from simulations.

Patch connectivity (mm)	L_1	a (prey attacks·d ⁻¹)	T_h (d ⁻¹)	Predicted mortality at the following prey densities (prey·arena ⁻¹)		
				0.10	0.50	1.00
Two patches						
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 [†]	0.49±0.01***	0.10	0.49	0.85
Four patches						
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 patches						
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

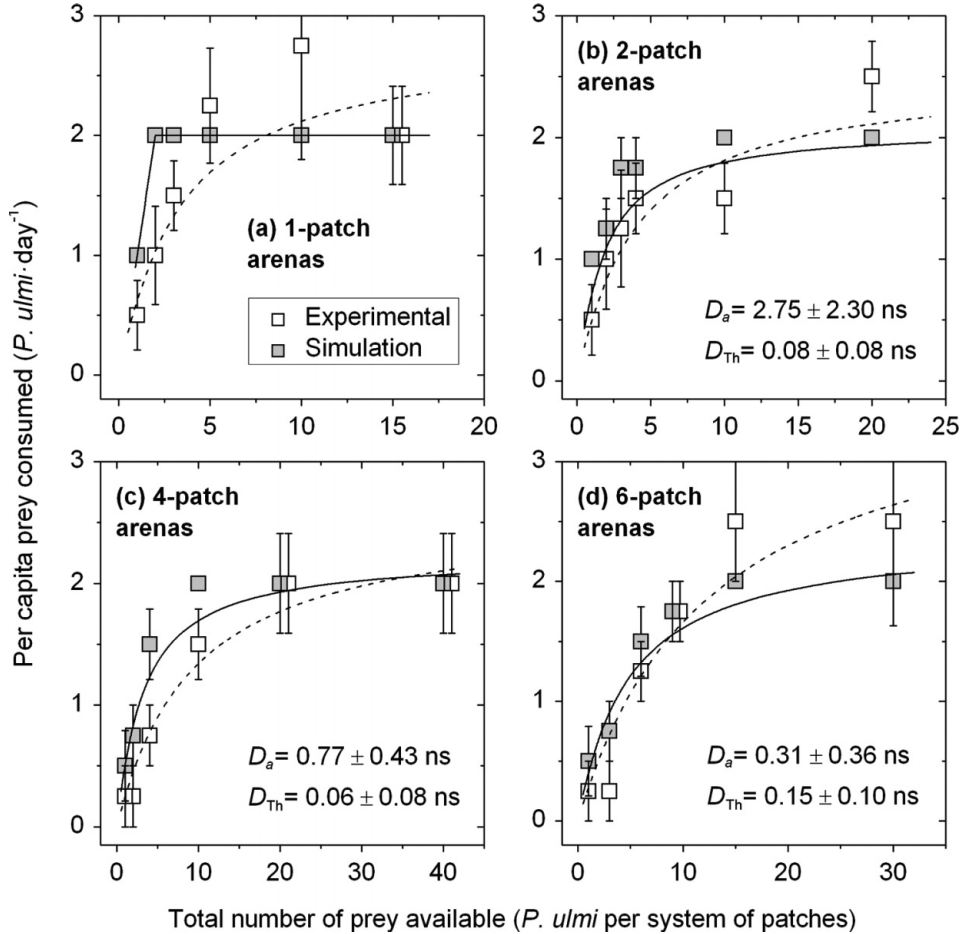
Note: The number of patches varied between simulations, as well as the connectivity which was modified by varying the diameter of the corridor connecting patches. Patch diameter, 30 mm. Also shown is the mortality predicted by these models at three chosen prey densities. Significance tests examine if the coefficient is significantly different from 0: ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values are estimates ± SE; $n = 6$ simulations.

[†]We were unable to obtain model convergence to the two-patch, 4-mm stem width simulation data. The data appeared to better approximate a type I functional response.

between the four- and six-patch systems. To test if such differences in a were significant, we statistically compared the estimate of a in the two- and six-patch systems with 0.25 mm connectivity. Estimates of D_a for this analysis confirmed a was significantly higher in the two-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 decline with increasing patch number (Tables 1 and 2). In accordance with the decreased attack rate, the predicted predation rates were lowest

Fig. 3. The functional responses of *A. fallacis* attacking *P. ulmi* on (a) one, (b) two, (c) four, or (d) six interconnected leaf systems. D_a and D_{T_h} are results from analyses testing for differences between the attack rates (a) and the handling times (T_h) of experimental and simulated data \pm SE; ns, no significant difference. Fitted lines are from the functional response equations, with the exception of the one-leaf simulated data, which appeared to be of a type I form. Analyses comparing a and T_h were thus not carried out for the one-leaf system. $n = 4$; error bars = 1 SE. Open squares and broken lines are data from experiments, whereas shaded squares and solid lines are data from simulations. Overlying points are offset slightly.



in the six-patch system. In the two-patch system with high connectivity nearly all available prey are predicted to be killed. In contrast in the six-patch system, only approximately half the available prey were killed 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 4-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 4.00 mm connectivity than in the 0.05 mm connectivity treatments of the four-patch system ($D_a = 3.12 \pm 1.26$; $P = 0.02$) (all 66 possible pairwise analyses of treatments in this data set were not analysed because of 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).

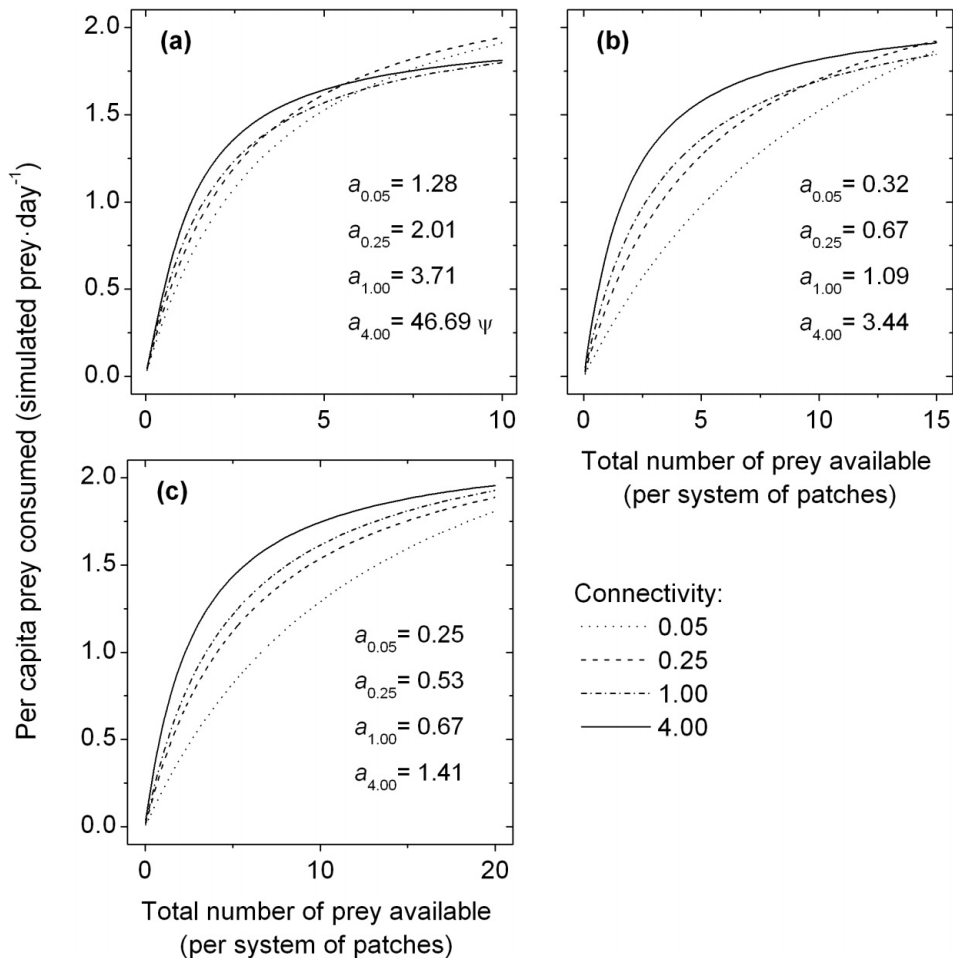
Slight differences observed in the handling time (T_h) for the simulated predator were not considered relevant here, as we programmed the predator with a constant handling time

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 behaviour 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 unexpected results were observed for both the experiments and simulations wherein predator-prey encounter rates were reduced to extremely low levels. We had suspected a type III response would be likely in simulations such as with the six-patch system and the lowest connectivity treatment of 0.05 mm. This degree of connectivity was 80 times lower than in the 4.00-mm treatment and correspondingly the simulated predator was observed to move

Fig. 4. Simulations of the functional response of predators on (a) two-, (b) four-, or (c) six-patch systems. The different lines on each graph represent simulations where the corridor between patches was increased from a radius of 0.05–4.00 mm, thus changing the likelihood of a predator (or prey) to move among patches. The parameters a represent attack rates (prey·day⁻¹) in the different simulations. The attack rate for 4.00 mm in the two-patch arena (ψ) was unable to be accurately estimated because of a lack of convergence.



among the treatments much less frequently. 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: (1) have we realistically estimated the functional response type and (2) 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 more natural, multipatch 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 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 and 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 predator–prey interaction changes with varying time to move successfully

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 can 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; Nunnery 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, modified type II 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 exhibit metapopulation dynamics in which local extinction on patches or even entire plants may not be of relevance, as recolonization events could 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 man-

agement of predators with type II functional responses, as each has vastly different implications. To enhance populations of phytoseiid predators or conserve other predators such as lynx, should we maintain metapopulation structure or encourage alternative prey species?

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