Variation in predator foraging behaviour changes predator-prey spatio-temporal dynamics

Punya Nachappa^{†,1}, David C. Margolies^{*,1}, James R. Nechols¹ and James F. Campbell²

¹Department of Entomology, Kansas State University, Manhattan, Kansas 66506, USA; and ²USDA-ARS Center for Grain and Animal Health Research, 1515 College Avenue, Manhattan, Kansas 66502, USA

Summary

1. Foraging underlies the ability of all animals to acquire essential resources and thus provides a critical link to understand population dynamics. A key issue is how variation in foraging behaviour affects foraging efficiency and predator–prey interactions in spatially heterogeneous environments. However, there is very little quantitative information available on this topic.

2. We evaluated the impact of variation in predator foraging on population dynamics of the predatory mite, *Phytoseiulus persimilis*, and its prey, the twospotted spider mite, *Tetranychus urticae*, in a heterogeneous environment.

3. Through artificial selection, we generated predator lines with high levels of prey consumption, conversion efficiency or dispersal, which were otherwise similar in foraging and life history. With these lines, we experimentally compared the effect of these traits on temporal and spatial patterns of predators and prey.

4. We initiated the experiments in a 24-plant landscape, which contained two discrete prey patches (i.e. prey-infested plants) under two initial predator-prey population ratios (1 : 10 and 1 : 30). Predators were introduced into one of the prey patches and were left to forage for 24 days.

5. Predator population growth was similar among the three selected lines, but the high conversion efficiency line produced the most predators and had the highest predator–prey ratio, and the high consumption and high dispersal lines were intermediate. The unselected line showed the least predator growth and lowest predator–prey ratio throughout the experiment.

6. Initial predator-prey ratio did not affect the impact of the selected lines on prey population growth at the high (1 : 10) ratio. However, at the low predator-prey ratio (1 : 30), the unselected line had a much greater prey numbers than the selected lines.

7. Predators and prey were each individually aggregated, but the high conversion efficiency and high dispersal lines showed stronger spatial association and correlation with prey, while the high consumption line was less closely associated or correlated with the prey.

8. These results indicate that there may be multiple, equally effective strategies by which predators exploit prey in patchy landscapes, but suggest that the long-term dynamics may not be stable under all of these strategies.

Key-words: foraging behaviours, genetic variation, population dynamics, predator-prey ratios, predatory mite, SADIE, twospotted spider mite

Introduction

A key unresolved question concerning predator-prey interactions is how predator foraging strategy affects predatorprey dynamics, especially in spatially heterogeneous

*Correspondence author. E-mail: dmargoli@k-state.edu

environments (Ives 1995; Roitberg & Mangel 1997; Morales & Ellner 2002). Spatial heterogeneity, in terms of the distribution of prey patches, is important to predator foraging for several reasons. First, patchily distributed prey presents a challenge for individual predators seeking food (Tscharntke & Kruess 1999; Walde & Nachman 1999). Second, the pattern of predation among patches of prey influences population dynamics of predators and prey (Ellner

[†]Present address. Department of Entomology, Texas A & M University, College Station, Texas 77843, USA.

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et al. 2001; Bell *et al.* 2009). Finally, the stability of predator-prey interactions may be increased when prey have a patchy distribution (May 1978; Comins & Hassell 1979). Thus, predator foraging provides a conceptual and mechanistic link between the structure of the environment and predator-prey population dynamics, especially in fragmented or changing environments.

Regional dynamics of predator-prey interactions depend in large part on local dynamics within prey patches (Bonsall, French & Hassell 2002; Hauzy et al. 2007). A local prey patch can be considered a homogeneous resource, within which the predator-prey interaction is described by Lotka-Volterra parameters such as the rate at which predators consume prey and the efficiency with which predators convert their food (i.e. prey) into offspring. In landscapes composed of many prey patches, the local, or within-patch, predator consumption rate and conversion efficiency also affect regional or among-patch dynamics because by affecting local per capita prey availability, they affect the timing and magnitude of predator dispersal from the patch. Although the local predator growth rate is reduced when predators disperse from a patch, colonization of other prey patches ultimately contributes to greater predator productivity at a regional scale (Van Baalen & Sabelis 1995). Thus, predator consumption, conversion efficiency and dispersal are important to both local and regional dynamics and interact to affect the stability of predator-prev interactions (Berryman & Gutierrez 1999).

Models of prey exploitation that assume a homogeneous environment commonly consider predator foraging strategies that differ only in the rate of predation. Under that scenario, when predators and prey are homogeneously mixed in the environment, natural selection should favour predators with the highest consumption and population growth rates (Maynard Smith 1982), although in the long run, this may cause predator-prey dynamics to become unstable because prey are overexploited (May 1972). However, when there is spatial structure in both predators and prey distribution, alternatives to a high consumption strategy, such as high conversion efficiency or rate of emigration from a local habitat, might be advantageous (Van Baalen & Sabelis 1995; Pels, de Roos & Sabelis 2002). The best strategy would depend on the degree to which predators exploit local prey populations, which in turn depends on the spatial distribution of prey in the landscape, the number of migrants and the stochastic nature of the colonization process (Pels, de Roos & Sabelis 2002).

Limited quantitative information is available concerning the interrelations between spatial distribution of predators and prey and population dynamics (Bell *et al.* 2009), and even less is known about how predator foraging traits affect these processes. However, theoretical treatments (Hassell & May 1985; Pels, de Roos & Sabelis 2002) and empirical evidence (e.g. Takafuji 1977; Murdoch, Briggs & Nisbet 1996; Hanski *et al.* 2004) suggest that even small differences in predator efficiency, because of differences in foraging strategy or landscape structure, might greatly alter population dynamics of predator and prey. We chose to examine the impact of predator consumption rate, conversion efficiency and dispersal on both predator and prey dynamics in patchy landscapes. We focussed on these traits because we expected that each of them could affect the balance between local and regional predatorprey dynamics in a different way. For example, in a landscape containing more than one prey patch, a high consumption phenotype should have a greater impact than other phenotypes on local prey densities; we might expect this predator to exhibit a high degree of aggregation in a local patch, but less spatial association with prey regionally. Predators with a high dispersal tendency should rapidly colonize distant prey patches, resulting in a more positive spatial association with prey at the regional level, but a less impactful predator-toprey ratio locally, than other phenotypes. Because a high conversion phenotype would produce more offspring per prey consumed, we might expect these predators to increase in a local patch more rapidly than the other phenotypes and disperse to new patches in search of food once local carrying capacity is exceeded. Hence, a high conversion phenotype would be more positively associated with prev both locally and regionally, causing a greater reduction in prey numbers than any other predator line.

Specifically, our aim was to investigate the role of these traits on the spatial and temporal dynamics of a predatory mite, Phytoseiulus persimilis Athias-Henriot (Fig. 1), and its herbivorous prey, the twospotted spider mite, Tetranychus urticae Koch. This interaction offered several advantages for studying how foraging links landscape structure and population dynamics. Firstly, the relationship between consumption and reproduction by the predators was simple; P. persimilis feeds and reproduces exclusively on spider mites, and there is a linear relationship between the number of prey consumed and the number of predator offspring produced (Sabelis 1981; Nachappa et al. 2010). Secondly, the spatial interactions were tractable; spider mites occur in discrete patches, and predators primarily move among patches by walking. Thirdly, the system was easy to manipulate; whole plants can be arranged in spatial designs that reflect the 'natural' environment in which the species interact. And lastly, we had



Fig. 1. Image of adult female, *Phytoseiulus persimilis* (picture by Greg Zolnerowich, Kansas State University).

available three lines of *P. persimilis*, each of which exhibited a high level of one of the three above-mentioned traits but were otherwise similar in foraging and life history (Nachappa *et al.* 2010). These lines provided material to test hypotheses about the role of foraging in population dynamics through the power of manipulative experiments (Anholt 1997). Moreover, although others have used artificial selection to study individual foraging traits, our development of multiple lines that were homogeneous except for a specific foraging trait gave us a unique opportunity to experimentally compare the impact of each of these traits on predator–prey dynamics in a patchy landscape.

Materials and methods

STUDY SPECIES

The predatory mite, P. persimilis (Acari-Mesostigmata-Phytoseiidae), is an extreme feeding specialist, requiring spider mites for development and reproduction (McMurtry & Croft 1997) (Fig. 1). This predator is thought to be of Mediterranean or South American origin (Dosse 1958), but it has been established in many parts of the world since the 1960s as a biological control agent primarily for twospotted spider mites (Van Lenteren & Woets 1988). Adult females normally consume one prey per hour (Sabelis 1981; Nachappa et al. 2010), whereas immatures and adult males feed much less (Bancroft & Margolies 1996). When these predators find a spider mite colony, they tend to concentrate searching and feeding in that area until all the prey have been killed, after which the predators disperse. While prey are available, the predator sex ratio is female-biased, usually close to 0.83, and each female can produce 60 eggs in her lifetime (Helle & Sabelis 1985). Phytoseiulus persimilis has five developmental stages: egg, nonfeeding larva, protonymph, deutonymph and adult (Sabelis 1981). Under the temperature conditions maintained in our experiments, development time (egg to adult) at 25 °C is 3-4 days, generation time (egg to egg) is 5-7 days and average adult lifespan is 25 days (Takafuji & Chant 1976); adult females consume prey and oviposit at a relatively constant level throughout their adult life.

Their prey, the twospotted spider mite, T. urticae (Acari-Prostigmata-Tetranychidae), is a generalist herbivore with a world-wide distribution (Van de Vrie, McMurtry & Huffaker 1972). Spider mites have five stages of development: egg, larva, protonymph, deutonymph and adult. The population goes through a generation every 7-10 days (Sabelis 1981). Adult female T. urticae are relatively sedentary after an initial teneral dispersive phase (Bancroft & Margolies 1996), and as long as hosts are available, most dispersal that does occur is short-distance ambulation (Nachman 1981). They mainly colonize the underside of leaves where they produce webbing in which all stages live and most activity (e.g. feeding, mating and oviposition) takes place; in this way, clusters, or patches, of spider mites develop. The twospotted spider mites we used in our experiments were taken from a laboratory colony maintained on lima bean plants (Phaseolus lunatus L. cv. 'Sieva') at 24 °C, 60-70% relative humidity, 16 : 8 h (L-D) photoperiod.

We derived selected lines of *P. persimilis* population from a population purchased from Koppert Biological Systems, Inc. (Romulus, MI, USA), a commercial supplier of beneficial arthropods. Artificial selection was imposed following Nachappa *et al.* (2010) to create lines that exhibited a high level of one of three traits: consumption rate, conversion efficiency or dispersal response (see Appendix S1;

Tables S1 and S2, Supporting information). All lines were maintained on spider mites in separate 2-L mason jars in climate-controlled growth chambers under temperature and humidity conditions as described previously for spider mites. Voucher specimens of the Koppert population and derived lines were deposited in the Kansas State University Museum of Entomological and Prairie Arthropod Research under lot number 154.

INITIAL PREDATOR-PREY RATIO

The outcome of predator-prey dynamics in patchy environments may depend on starting conditions (Kean & Barlow 2000). In this regard, we were particularly interested in the effect of initial predator-prey ratios, which can affect time to extinction under different conditions of fragmentation (Holyoak & Lawler 1996). Thus, we examined predator-prey dynamics at two initial predator-prey release ratios, which can be thought of as reflecting predator invasion of spider mite patches either early or late in the population cycle. Studies of predation by P. persimilis on spider mites have shown that spider mites rapidly become extinct at a predator-prey release ratio of 1: 10 (Markkula & Tiittanen 1976), whereas at a predator-prey ratio of 1: 30, the effect of the predators on spider mite populations is variable (Opit, Nechols & Margolies 2004). We expected that, if the selected traits affected predator-prey dynamics, we would observe larger differences in spider mite numbers at a 1 : 30 predator-prey ratio than at 1:10.

EXPERIMENTAL DESIGN

The experimental design was a repeated measures 4×2 factorial with four foraging traits (three selected lines plus an unselected control) and two initial predator–prey release ratios (1 : 10 and 1 : 30) as factors. Data were collected four times (6, 12, 18 and 24 days after the introduction of predators) during the experiment. The experiment or block in its entirety was repeated three times from spring 2007 through spring 2008.

An experimental unit consisted of 24 bean plants each in a 15.2-cm pot arranged in an 8 × 3 array. Plants within an array were packed together as closely as possible to allow mites to move directly from plant to plant. Each plant array was set in a moat to inhibit mites from leaving and to isolate treatment combinations from each other (Opit, Nechols & Margolies 2004), with a minimum of 3 m between arrays. We conducted all trials in a 69.4-m² greenhouse at the Throckmorton Plant Sciences Center at Kansas State University, Manhattan, KS, USA. The greenhouse held four benches, each of which held two arrays, allowing us to run eight arrays in each trial, one for each treatment combination. Daily temperatures and relative humidity (RH) (mean \pm standard error) for each repetition of the experiment were the following: block 1, 24.25 \pm 3.27 °C, 52.17 \pm 15.89% RH; 23.89 ± 4.19 °C, $40.36 \pm 14.12\%$ RH; block 3, block 2. 25.79 ± 6.66 °C, $42.26 \pm 12.27\%$ RH. The average length of day and night (light-dark) was 16:8 (L-D) h under artificial lighting.

The experiment was designed so that all plant arrays started with similar numbers of prey divided between two plants, one at each end of the array (i.e. its long axis). Ten days prior to assembling the plants into arrays, 10 adult female spider mites were introduced to each of the plants that were to serve as initial prey patches. Prior to starting the experiment, the number of prey was estimated by counting only adult females on each plant. Prey patch plants were added to the array, and then we released adult female predators (7–10 days old) in one of the two prey patches per array. The number of predators

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released was adjusted so that we achieved the appropriate overall predator-prey ratio based on pre-release counts of prey. The numbers of adult prey and predators were counted on each plant in an array once every 6 days for 24 days. Experiments ended after 24 days because, by then, many plants showed substantial spider mite feeding damage and were no longer suitable hosts for the prey. This duration is coincident with the lifespan of a predatory mite and encompasses approximately three predator generations.

SPATIAL ANALYSES

To determine the distribution patterns of predatory mites and spider mites, we used SADIE (Spatial Association using Distance IndicEs; Perry 1995; Perry et al. 1996), a program available as a free download at http://www.rothamsted.bbsrc.ac.uk/pie/sadie/SADIE home page_1.htm. This methodology was developed explicitly for the spatial analysis of ecological data in the form of spatially referenced counts (Perry et al. 1999) and provides a means to measure the overall spatial pattern for a single set of data and spatial association for two sets of data, e.g. location of predatory mites and spider mites (Appendix S2, Supporting information). The aggregation index for single data sets, $I_{\rm a}$, is calculated such that a value of $I_{\rm a} \approx 1$ is associated with a spatially random pattern, $I_a > 1$ with a more aggregated pattern and $I_a < 1$ with a more regular pattern (Perry *et al.* 1999). The measure of spatial association between two data sets is represented by X, such that X > 0 for positively associated populations, $X \approx 0$ for populations positioned at random with respect to one another and X < 0 for negatively associated populations. The randomization method (Perry et al. 1999; Perry & Dixon 2002) was used to construct a formal test of significance in spatial association. The null hypothesis tested was that the spatial arrangement of predators was random with respect to prey (i.e. no spatial association). All SADIE statistics were generated with SADIESHELL v.1.5.3 (Rothamsted Experimental Station, Harpenden, Herts, UK).

STATISTICAL ANALYSES

Response variables from each 24-plant array were the following: (i) total number of predators; (ii) total number of prey; (iii) separate SADIE aggregation indices (I_a) for predators and prey; (iv) SADIE spatial association index (X); and (v) correlation between predator and prey numbers per plant (calculated as Pearson's correlation

coefficient, *r*). The experimental design was a randomized complete block design with repeated measures. A generalized linear mixedmodel analysis was conducted in a three-way ANOVA using foraging trait, ratio and sampling time (6, 12, 18 and 24 days), and their interaction as fixed effects and block as random effects. Sampling time was also a repeated measures factor. *F*-tests for fixed effects and *t*-tests for pairwise comparisons were performed based on the chosen correlation structure (Littell *et al.* 1996). The predator and prey counts were log₁₀-transformed prior to analyses to satisfy assumptions of ANOVA. All tests used a 0.05 type I error rate. All computations were carried out using PROC MIXED in SAS (SAS Institute 2001).

Results

ARTHROPOD COUNTS

Predators

Of the main effects, only foraging trait and time significantly affected predator counts (Table 1). There were significant differences in the pattern of population growth and final predator densities among the different predator lines (Fig. 2). The high conversion efficiency line produced more offspring than the high consumption ($t_{62} = 1.91$, P = 0.05), high dispersal ($t_{62} = 1.89$, P = 0.05) and unselected control line ($t_{62} = -4.40$, P < 0.0001). The high dispersal and high consumption lines were not different from each other in predator counts ($t_{62} = -0.01$, P = 0.99). There were significant differences in predator counts among the selected lines at day 18 ($t_{62} = 3.0$, P = 0.004) and day 24 ($t_{62} = 10.72$, P < 0.0001) (Fig. 2).

Prey

Initial spider mite densities per patch were 43.7 ± 3.3 , 44.9 ± 1.9 and $52.4 \pm 6.4.9$ (mean \pm standard error) for experiments (blocks) 1, 2 and 3, respectively. Analysis of subsequent counts found that all interactions and main effects were highly significant for prey numbers with the exception of foraging trait-release ratio, which was not significant

	Number		Aggregation in	$dex(I_a)$
Effect	Predator	Prey	Predator	Prey
Foraging trait	$F_{3,62} = 6.50$	$F_{3,62} = 6.84$	$F_{3,62} = 2.51$	$F_{3,62} = 1.03$
	P = 0.0007	P = 0.0005	P = 0.07	P = 0.39
Ratio	$F_{1.62} = 0.61$	$F_{1.62} = 22.09$	$F_{1.62} = 4.42$	$F_{1.62} = 0.39$
	P = 0.44	P < 0.0001	P = 0.04	P = 0.53
Foraging trait × ratio	$F_{3.62} = 1.77$	$F_{3.62} = 2.39$	$F_{3.62} = 1.39$	$F_{3.62} = 0.95$
	P = 0.16	P = 0.07	P = 0.25	P = 0.42
Time	$F_{3.62} = 75.48$	$F_{3.62} = 83.16$	$F_{3.62} = 5.38$	$F_{3.62} = 6.21$
	P < 0.0001	P < 0.0001	P = 0.002	P = 0.0009
Foraging trait × time	$F_{9.62} = 1.57$	$F_{9.62} = 5.12$	$F_{9.62} = 2.40$	$F_{9.62} = 0.80$
0 0	P = 0.14	P < 0.0001	P = 0.02	P = 0.62
Ratio \times time	$F_{3,62} = 0.06$	$F_{3,62} = 5.12$	$F_{3.62} = 2.51$	$F_{3.62} = 0.63$
	P = 0.98	P = 0.0032	P = 0.07	P = 0.60
Foraging trait ×	$F_{9.62} = 0.37$	$F_{9.62} = 4.0$	$F_{9.62} = 0.59$	$F_{9.62} = 0.76$
ratio × time	P = 0.94	P = 0.0005	P = 0.80	P = 0.65

Table 1. Significance of foraging trait, predator release ratio and time on abundance and distribution of predator (*Phytoseiulus persimilis*) lines and their prey (*Tetranychus urticae*). *P*-values highlighted in bold are significant

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Fig. 2. Number of predators (mean \pm SE) at 6-day intervals for 24 days in a 24-plant array.

(Table 1). At a predator release ratio of 1 : 10, there were no significant differences between the selected lines and the unselected line at any of the sampling times (Fig 3a). However, at a predator release ratio of 1 : 30, the unselected line had greater prey counts than the high conversion line $(t_{62} = -2.06, P = 0.04)$ and high consumption line $(t_{62} = 2.55, P = 0.02)$, but the unselected line was not different than the high dispersal line $(t_{62} = 1.09, P = 0.28)$, at day 18 (Fig. 3b). At day 24, the unselected line had greatest final prey densities compared with the selected lines (all P < 0.0001; Fig. 3b).

Overall, the prey numbers were lower at the predator release ratio of 1 : 10 than 1 : 30 at days 12 ($t_{62} = -4.04$, P < 0.0001), 18 ($t_{62} = -2.75$, P = 0.01) and 24 ($t_{62} = -7.34$, P < 0.0001) (Fig. 3a,b).

AGGREGATION OF EACH SPECIES

Predators

The only significant interaction with respect to predator aggregation was the two-way interaction between foraging trait and time (Table 1). Predator spatial distributions were aggregated throughout ($I_a > 1$), but change in the degree of aggregation over time varied between lines (Fig. 4). Aggregation of the unselected control continuously increased; aggregation of the high consumption line increased until day 18 and then decreased, while aggregation of the high conversion efficiency and high dispersal lines increased only slightly with some fluctuation. On day 18, the high consumption line was significantly more aggregated than the high conversion

efficiency line ($t_{62} = 2.81$, P = 0.01) and the high dispersal line ($t_{62} = 2.54$, P = 0.01), while the unselected line was not more aggregated than the high conversion efficiency line ($t_{62} = 1.93$, P = 0.06) or the high dispersal line ($t_{62} = 1.90$, P = 0.09). On day 24, there were no differences between the high conversion efficiency, high consumption and high dispersal lines, but all were significantly less aggregated than the unselected control ($t_{62} = 2.99$, P = 0.004, $t_{62} = 3.70$, P = 0.001 and $t_{62} = 2.44$, P = 0.02, respectively).

Prey

There were no significant interactions in prey aggregation and, of the main factors, only time had a significant effect on distribution of prey populations (Table 1). Prey populations were significantly aggregated ($I_a > 1$) throughout and exhibited increasing aggregation as the experiment progressed.

SPATIAL ASSOCIATION OF PREDATORS AND PREY

There were no significant interactions among main effects in the spatial association of predators and prey (Table 2). The average spatial association of predators and prey was positive for all lines (mean spatial association \pm SE, $X = 0.03 \pm 0.15$ for the high consumption line, 0.20 ± 0.08 for the high conversion efficiency line, 0.29 ± 0.12 for the high dispersal line and 0.05 ± 0.14 with the unselected control). The high dispersal line had higher average spatial association with prey than the unselected control ($t_{62} = -2.23$, P = 0.03) or high consumption line ($t_{62} = -2.45$, P = 0.02), but the high dispersal line was not different than the conversion efficiency line ($t_{62} = -0.88$, P = 0.38). Spatial association of predator and prey decreased over the first three sampling periods (6, 12 and 18 days) but then increased in the last sample period, 24 days (Fig. 5). A visual example of spatial association maps and numerical correlation of predators and prey is presented in Fig. S1 (Supporting information).

CORRELATION BETWEEN PREDATOR AND PREY NUMBERS

Analysis of correlation between predator and prey numbers per plant was similar to the spatial association analysis (Table 2). There were no significant interactions among any of the main effects. The conversion efficiency line (mean



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Fig. 4. Aggregation (I_a) of predators (mean \pm SE) at 6-day intervals for 24 days in a 24-plant array.

Table 2. Significance of foraging trait, predator release ratio and time on the spatial association and correlation coefficient of predator (*Phytoseiulus persimilis*) lines and their prey (*Tetranychus urticae*). *P*-values highlighted in bold are significant

Effect	Spatial association index (X)	Correlation coefficient (<i>r</i>)
Foraging trait	$F_{3,62} = 2.67$	$F_{3,62} = 5.58$
	P = 0.05	P = 0.002
Ratio	$F_{1,62} = 0.03$	$F_{1,62} = 0.16$
	P = 0.86	P = 0.69
Foraging trait × ratio	$F_{3.62} = 0.30$	$F_{3.62} = 0.76$
	P = 0.82	P = 0.52
Time	$F_{3.62} = 5.72$	$F_{3.62} = 2.60$
	P = 0.0016	P = 0.05
Foraging trait × time	$F_{9.62} = 1.73$	$F_{9.62} = 0.88$
	P = 0.10	P = 0.55
Ratio × time	$F_{3.62} = 0.68$	$F_{3.62} = 1.26$
	P = 0.57	P = 0.30
Foraging trait ×	$F_{9.62} = 0.29$	$F_{9.62} = 0.46$
ratio × time	P = 0.97	P = 0.90

correlation \pm SE, $r = 0.33 \pm 0.04$) was not different from the dispersal line (mean correlation \pm SE, $r = 0.33 \pm 0.037$) ($t_{62} = -0.03$, P = 0.98), but both were more positively correlated with prey than was the unselected (mean correlation \pm SE, $r = 0.16 \pm 0.02$) control $(t_{62} = 2.71, P = 0.001 \text{ and } t_{62} = -3.43, P = 0.001, \text{ respec-}$ tively) and the high consumption line (mean correlation \pm SE, $r = 0.23 \pm 0.039$) ($t_{62} = 2.05$, P = 0.04 and $t_{62} = -2.02$, P = 0.05, respectively). We detected strong positive correlations for all predator lines at days 6 and 12, no relationship at day 18 and strong correlation again at day 24 (mean correlation \pm SE, r, day 6: 0.37 \pm 0.04, day 12: 0.29 ± 0.04 , day 18: 0.10 ± 0.06 and day 24: 0.29 ± 0.08) (all P < 0.0001 except day 18, $t_{62} = 1.63$, P = 0.11).

Discussion

Spatial coincidence of predators and prey is key to their interaction and population dynamics. In environments in which prey are distributed in discrete patches which change in



Fig. 5. Spatial association (X) between predators and prey (mean \pm SE) at 6-day intervals for 24 days in a 24-plant array.

location and abundance over time, the location and abundance of predators may not consistently correlate with their prey. This presents a challenge to individual predators, whose success depends on their foraging strategy in relation to the abundance and distribution of resources (Heinz & Strand 2006). This situation also challenges populations of both predators and prey, whose persistence also depends in large part on predator foraging strategy (Huffaker 1958; Beddington, Free & Lawton 1975; Murdoch & Oaten 1989). We posed two questions regarding predator-prey interactions faced with such challenges: Is there a single foraging strategy that is likely to be most successful in a patchy environment? To what extent do predator-prey dynamics respond to predator foraging strategy in patchy environments? To address these questions, we established a simple patchy distribution of the twospotted mite, T. urticae, and compared temporal and spatial dynamics of its interaction with predatory mite, P. persimilis, using different artificially generated predator foraging phenotypes and two predator-prey release ratios. We expected that the effects of resource heterogeneity on individuals and populations would depend on the behaviour and demography of predators using that resource (Kareiva 1987). Our results indicated that the foraging strategies by which predators exploited prey in this simple patch system affected both short-term success of specific phenotypes and the dynamics of the interacting populations.

Temporal dynamics of the predator–prey interaction in a patch are likely to be affected by the initial predator–prey ratio, with subsequent effects on the duration of the predator–prey interaction and production of dispersive propagules (Pels, de Roos & Sabelis 2002). In our study, the initial predator–prey ratio (1 : 10 or 1 : 30) had the expected effect on prey dynamics under the unselected line, but such an effect was absent under any of the selected lines. That is, when initial predator density was high relative to prey (1 : 10), as would be the case when predators invade a recently founded prey patch, predator foraging strategy did not affect prey population dynamics. High predator numbers within a patch eclipsed differences in individual consumption rate and conversion efficiency, and prey were exploited quickly enough

that predator dispersal rates were high in all lines. However, when initial predator density was low relative to prey (1: 30), as might be the case when predators found a more mature prey colony, prey numbers increased two to threefold more under the unselected line, while prey dynamics under all three selected lines were similar to that seen at the higher ratio. Predators exhibiting high consumption, high conversion efficiency or high dispersal were able to compensate for their initial low density either by having high average attack rates (Fig. 3b), with immediate effect on prey numbers, or by having high average reproductive rates (Fig. 2), with an impact over time. The latter effect was particularly apparent under the high conversion line. As expected, the high conversion efficiency line had a higher reproductive output in total than did the high consumption line. This was in contrast to previous research (Nachappa et al. 2010) that found the high consumption and conversion lines were equivalent in local patches. This highlights how the inclusion of a landscape pattern changes the outcomes predicted from a single patch or simpler system.

Spatial dynamics, meaning the distribution of attack and reproduction among patches, also contributed to the efficiency of the selected lines independent of the initial predator-prey ratio. Predators started and remained aggregated throughout the experiments regardless of their foraging strategy (Fig. 4). Prey, however, while initially aggregated, became more evenly distributed over time. Prey would become more uniformly distributed, even in the absence of predators, simply because they must spread from the initial patches as they consumed plants. In addition, in the presence of predators, prey may disperse to avoid predation (Onzo et al. 2003). Furthermore, predators can cause a more even or uniform prey distribution directly by predation on high-density prey patches, while prey in less dense patches are left to persist and increase (Wilson et al. 1984). It is most likely that changes we observed in prey aggregation under selected lines resulted primarily from direct reduction in prey in the initial patch; a visual comparison of prey spread from the patch into which predators were released with that from the patch without predators (Fig. S1, Supporting information) suggests that predators decreased the rate at which prey spread.

As prev distribution became more uniform, spatial association between predators and prey became less positive, as suggested in a theoretical model by Bell et al. (2009). However, we found that changes in patterns of spatial coincidence between predators and prey depended on the foraging strategy of the predators that were released into the system (Fig. 5). Predators from the high conversion efficiency and dispersal lines showed more positive spatial association and numerical correlation with prey than did predators from the high consumption and the unselected control populations. Both of the former lines did better at tracking prey than the unselected control (because of lower numbers) and high consumption (because of lower dispersal). However, even similar patterns of association appear to have been generated by different processes in each line. For instance, while both the high dispersal and high conversion efficiency lines were able to find

and utilize new prev patches, predators from the high dispersal line did so because they tended to leave prey patches sooner than the other lines (Nachappa et al. 2010), while predators from the high conversion efficiency line produced more offspring locally, which then dispersed to find new prey as they depleted local resources. This resulted in better tracking of prey density by the high conversion efficiency line than other lines despite their average dispersal rate from a prey patch (Table S1, Supporting information). In contrast, predators from the high consumption line remained within a prey patch and consumed more prey locally than other lines, which delayed their dispersal and colonization of unexploited prey patches. The high consumption line had a strong negative association with prey at 18 days (Fig. 5), which suggests that they drove down prey in patches to a greater extent than the other lines, so predators remained in patches with fewer prey while prey populations were able to grow elsewhere. By the end of the experiment, the control was the most poorly associated with prey; this lack of association was probably due to large increases in prey populations while predator numbers remained relatively low.

In effect, the high conversion efficiency line exhibited the most effective foraging attributes of both the high consumption and high dispersal lines; high conversion efficiency predators produced more progeny than the other lines, which increased the local predator-prey ratio while at the same time resulted in more dispersers. This might make predators with the high conversion efficiency trait more successful at immediately exploiting local prey patches and locating new patches. However, simulations of a large-scale metapopulation model showed that selection for high conversion efficiency leads to the extinction of prey and predators in a patchy environment, while selection for higher consumption or emigration rates allows the predator-prey interaction to persist (Pels, de Roos & Sabelis 2002). Compared with consumption, emigration is a more likely target for selection to achieve persistent exploitation. Although our study was conducted in a limited landscape with only two prey patches initially, our results support this outcome for stability and persistence of predator-prey dynamics in larger landscapes.

In landscapes consisting of many patches, the effects of patchiness on population dynamics depend on population processes occurring within local patches (Bonsall, French & Hassell 2002; Ryall & Fahrig 2006). Dispersal in particular is crucial to the dynamics of spatially structured populations (Liebhold, Koenig & Bjornstad 2004; Hauzy et al. 2007). Specifically, the timing and intensity of dispersal from local patches can affect the persistence of a predator-prey interaction (Huffaker 1958; Zeigler 1977; Crowley 1981; Nachman 1987; Holyoak & Lawler 1996); successful colonization of new patches is related to the number of dispersers produced in predator-occupied patches (Sabelis et al. 1999). However, the effect of patchiness on regional persistence depends on the foraging behaviour of the predators (Kareiva 1987). Regional persistence of predators and prey is most likely to occur when the dynamics within local patches are asynchronous (Huffaker 1958; van de Klashorst et al. 1992; Holyoak & Lawler

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1996; Janssen *et al.* 1997). Deciphering the effect of foraging traits on a population level in a predator–prey system should lead to a better understanding of the population dynamics (Bernstein, Kacelnik & Krebs 1988; Werner 1992; Bell *et al.* 2009) and address the adaptive nature of specific phenotypes in an ecological context (Brakefield 2003).

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References

- Anholt, B.R. (1997) How should we test for the role of behaviour in population dynamics. *Evolutionary Ecology*, 11, 633–640.
- Bancroft, J.S. & Margolies, D.C. (1996) Allocation of time between feeding, resting, and moving by the twospotted spider mite and is predator *Phytoseiulus persimilis. Experimental and Applied Acarology*, 20, 391–404.
- Beddington, J.R., Free, C.A. & Lawton, J.H. (1975) Dynamic complexity in predator-prey models framed in difference equations. *Nature*, 255, 58–60.
- Bell, A.V., Rader, R.B., Peck, S.L. & Sih, A. (2009) The positive effects of negative interactions: can avoidance of competitors or predators increase resource sampling by prey? *Theoretical Population Biology*, 76, 52–58.
- Bernstein, C., Kacelnik, A. & Krebs, J.R. (1988) Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecol*ogy, 57, 1007–1026.
- Berryman, A.A. & Gutierrez, A.P. (1999) Dynamics of insect predator-prey interactions. *Ecological Entomology*, 2nd edn (eds C.B. Huffaker & A.P. Gutierrez), pp. 389–420. John Wiley and Sons, New York.
- Bonsall, M.B., French, D.R. & Hassell, M.P. (2002) Metapopulation structures affect persistence of predator-prey interactions. *Journal of Animal Ecology*, 71, 1075–1084.
- Brakefield, P.M. (2003) Artificial selection and the development of ecologically relevant phenotypes. *Ecology*, 84, 1661–1671.
- Comins, H.N. & Hassell, M.P. (1979) The dynamics of optimally foraging predators and parasitoids. *Journal of Animal Ecology*, 48, 335–351.
- Crowley, P.H. (1981) Dispersal and the stability of predator-prey interactions. *The American Naturalist*, **118**, 673–701.
- Dosse, G. (1958) Über einige neue Raubmilbenarten (Acar. Phytoseiidae). *Pflanzenschutzberichte*, **21**, 44–61.
- Ellner, S.P., McCauley, E., Kendall, B.E., Briggs, C.J., Hosseini, P.R., Wood, S.N., Janssen, A., Sabelis, M.W., Turchin, P., Nisbet, R.M. & Murdoch, W.W. (2001) Habitat structure and population persistence in an experimental community. *Nature*, **412**, 538–542.
- Hanski, I., Erälahti, C., Kankare, M., Ovaskainen, O. & Sirén, H. (2004) Variation in migration rate among individuals maintained by landscape structure. *Ecology Letters*, 7, 958–966.
- Hassell, M.P. & May, R.M. (1985) From individual behavior to population dynamics. *Behavioural Ecology* (eds R.M. Sibly & R.H. Smith), pp. 3–32. Blackwell Scientific Publications, Oxford, UK.
- Hauzy, C., Hulot, F.D., Gins, A. & Loreau, M. (2007) Intra- and interspecific density-dependent dispersal in an aquatic prey-predator system. *Journal of Animal Ecology*, **75**, 552–558.
- Heinz, S.K. & Strand, E. (2006) Adaptive patch searching strategies in fragmented landscapes. *Evolutionary Ecology*, 20, 113–130.
- Helle, W. & Sabelis, M.W. (1985) Spider Mites, Their Biology, Natural Enemies and Control. World Crop Pests, Vol. 1B. Elsevier, Amsterdam.
- Holyoak, M. & Lawler, S.P. (1996) The role of dispersal in predator-prey metapopulation dynamics. *Journal of Animal Ecology*, 65, 640–652.
- Huffaker, C.B. (1958) Experimental studies on predation, dispersion factors and predator-prey oscillations. *Hilgardia*, 27, 343–383.

- Ives, A.R. (1995) Spatial heterogeneity and host-parasitoid population dynamics, do we need to study behavior? *Oikos*, 74, 366–376.
- Janssen, A., van Gool, E., Lingeman, R., Jacas, J. & van de Klashorst, G. (1997) Metapopulation dynamics of a persisting predator-prey system in the laboratory, time series analysis. *Experimental and Applied Acarology*, 21, 415–430.
- Kareiva, P. (1987) Habitat fragmentation and the stability of predator-prey interactions. *Nature*, **326**, 388–390.
- Kean, J.M. & Barlow, N.D. (2000) The effects of density-dependence and local dispersal in individual-based stochastic metapopulations. *Oikos*, 88, 282– 290.
- Liebhold, A., Koenig, W.D. & Bjornstad, O.N. (2004) Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, 35, 467–490.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996). SAS System for Mixed Models. SAS Institute Inc, Cary, NC.
- Markkula, M. & Tiittanen, K. (1976) "Pest-in-first" and "natural infestation" methods in the control of *Tetranychus urticae* Koch with *Phytoseiulus persimilis* Athias-Henriot on glasshouse cucumbers. *Annales Agriculture Fennici*, 15, 81–85.
- May, R.M. (1972) Limit cycles in predator-prey communities. Science, 177, 900–902.
- May, R.M. (1978) Host-parasitoid systems in patchy environments, a phenomenological model. *Journal of Animal Ecology*, 47, 833–843.
- Maynard Smith, J. (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge.
- McMurtry, J.A. & Croft, B.A. (1997) Life-styles of phytoseiid mites and their roles in biological control. *Annual Review of Entomology*, 42, 291–321.
- Morales, J.M. & Ellner, S.P. (2002) Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, 83, 2240–2247.
- Murdoch, W.W., Briggs, C.J. & Nisbet, R.M. (1996) Competitive displacement and biological control in parasitoids: a model. *The American Naturalist*, 148, 807–826.
- Murdoch, W.W. & Oaten, A. (1989) Aggregation by parasitoids and predators, effects on equilibrium and stability. *The American Naturalist*, **134**, 288–310.
- Nachappa, P., Margolies, D.C., Nechols, J.R. & Morgan, T. (2010) Response of a complex foraging phenotype to selection on its component traits. *Evolu*tionary Ecology, 24, 631–655.
- Nachman, G. (1981) Temporal and spatial dynamics of an acarine predatorprey system. *Journal of Animal Ecology*, 50, 435–451.
- Nachman, G. (1987) Systems analysis of acarine predator-prey interactions. II. The role of spatial processes in system stability. *Journal of Animal Ecology*, 56, 267–281.
- Onzo, A., Hanna, R., Zannou, I., Sabelis, M.W. & Yaninek, J.S. (2003) Dynamics of refuge use, diurnal, vertical migration by predatory and herbivorous mites within cassava plants. *Oikos*, **101**, 59–69.
- Opit, G.P., Nechols, J.R. & Margolies, D.C. (2004) Biological control of twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) using *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseidae) on ivy geranium, assessment of predator release ratios. *Biological Control*, 29, 445– 452.
- Pels, B., de Roos, A.M. & Sabelis, M.W. (2002) Evolutionary dynamics of prey exploitation in a metapopulation of predators. *The American Naturalist*, 159, 172–189.
- Perry, J.N. (1995) Spatial analysis by distance indices. *Journal of Animal Ecology*, 64, 303–314.
- Perry, J.N. (1998) Measures of spatial pattern for counts. *Ecology*, 79, 1008– 1017.
- Perry, J.N. & Dixon, P. (2002) A new method for measuring spatial association in ecological count data. *Ecoscience*, 9, 133–141.
- Perry, J.N., Bell, E.D., Smith, R.H. & Woiwod, I.P. (1996) SADIE: software to measure and model spatial pattern. *Aspects of Applied Biology*, 46, 95– 102.
- Perry, J.N., Winder, L., Holland, J.M. & Alston, R.D. (1999) Red-blue plots for detecting clusters in count data. *Ecology Letters*, 2, 106–113.
- Roitberg, B.D. & Mangel, M. (1997) Individuals on the landscape: behavior can mitigate landscape differences among habitats. *Oikos*, 80, 234–240.
- Ryall, K.L. & Fahrig, L. (2006a) Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecology*, 87, 1086–1093.
- Sabelis, M.W. (1981) Biological Control of Two-Spotted Spider Mites Using Phytoseiid Predators. Part 1: Modeling the Predator–Prey Interaction at the Individual Level. Agricultural Research Reports 910, pp. 240. Pudoc, Wageningen, the Netherlands.
- Sabelis, M.W., van Baalen, M., Bruin, J., Egas, M., Jansen, V.A.A., Janssen, A.
 & Pels, B. (1999) The evolution of overexploitation and mutualism in

plant-herbivore-predator interactions and its impact on population dynamics. *Theoretical approaches to biological control* (eds B.A. Hawkins & H.V. Cornell), pp. 259–282. Cambridge University Press, Cambridge, UK.

- SAS Institute (2001) SAS User's Guide; Statistics, Version 8.2. SAS Institute, Cary, NC.
- Takafuji, A. (1977) The effect of the rate of successful dispersal of a phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) on the persistence in the interactive system between the predator and its prey. *Researches on Population Ecology*, 18, 210–222.
- Takafuji, A. & Chant, D.A. (1976) Comparative studies of two species of predacious phytoseiid mites (Acarina: Phytoseiidae), with special reference to their responses to the density of their prey. *Researches on Population Ecology*, **17**, 255–310.
- Tscharntke, T. & Kruess, A. (1999) Habitat fragmentation and biological control. *Theoretical Approaches to Biological Control* (eds B.A. Hawkins & H.V. Cornell), pp. 190–205. Cambridge University Press, Cambridge, UK.
- Van Baalen, M. & Sabelis, M.W. (1995) The milker-killer dilemma in spatially structured predator-prey interactions. *Oikos*, 74, 391–400.
- Van de Klashorst, G., Les Readshaw, J., Sabelis, M.W. & Lingeman, R. (1992) A demonstration of asynchronous local cycles in an acarine predator-prey system. *Experimental and Applied Acarology*, 14, 185–199.
- Van de Vrie, M., McMurtry, J.A. & Huffaker, C.B. (1972) Ecology of tetranychid mites and their natural enemies: a review. III. Biology, ecology and pest status, and host-plant relations of Tetranychids. *Hilgardia*, **41**, 343–432.
- Van Lenteren, J.C. & Woets, J. (1988) Biological and integrated pest control in greenhouses. *Annual Review of Entomology*, 33, 239–269.
- Walde, S.J. & Nachman, G. (1999) Dynamics of spatially-structured spider mite populations. *Theoretical Approaches to Biological Control* (eds B.A. Hawkins & H.V. Cornell), pp. 163–189. Cambridge University Press, Cambridge.
- Werner, E.E. (1992) Individual behavior and higher-order species interactions. *The American Naturalist*, 140(Suppl.), 5–32.
- Wilson, L.T., Hoy, M.A., Zalom, F.G. & Smilanick, J.M. (1984) Sampling mites in almonds: I. Within-tree distribution and clumping pattern of mites with comments on predator-prey interactions. *Hilgardia*, 52, 1–13.

Zeigler, B.P. (1977) Persistence and patchiness of predator-prey systems induced by discrete event population exchange mechanisms. *Journal of Theoretical Biology*, 67, 687–713.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Selection procedures used to generate predator foraging lines used in the current study.

Appendix S2. Spatial Analysis by Distance Indices (SADIE) methodology used to determine spatial patterns.

Figure S1. Examples of distribution of abundance and spatial association maps of predator lines and their prey.

Table S1. Levels (mean \pm SE) of predator foraging traits in selected lines and the unselected control.

Table S2. Levels (mean \pm SE) of predator foraging traits before and after each experiment in lines previously selected for that trait.

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