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Metapopulation dynamics of a persisting predator–prey system in the laboratory: time series analysis

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ABSTRACT

The scarcity of experimental evidence for the persistence of predator–prey systems at the metapopulation level inspired us to develop a simple predator–prey experiment that could be used for testing several theoretical predictions concerning persistence and its causes. The experimental system used consisted of one or several islands with small bean plants, the phytophagous mite *Tetranychus urticae* and the predatory mite *Phytoseiulus persimilis*. In the first experiment, one large system was used consisting of 90 small bean plants, prey and predators. The system persisted for only 120 days. Second, a system was used consisting of eight islands with ten plants each where the islands were connected by bridges. Two replicate experiments showed persistence for at least 393 days. The difference between the first and the second experiments suggests that the longer persistence is caused by a limited migration between the eight islands. Despite efforts to start both replicates of the second experiment with similar initial conditions, the dynamics of both replicates varied substantially. In one replicate the prey and predator numbers showed a trend through time, whereas the numbers fluctuated around a fixed value in the other replicate. A time series analysis of the data of the prey and predators showed the presence of periodicity with a lag of 8.5 weeks in one replicate, whereas such cyclic behaviour was not found in the other replicate. The differences between the two replicates suggest that it is difficult to perform experiments where one replicate is perturbed and the other serves as an undisturbed control. We suggest using a longer time series, where a system is disturbed only during the second half of the experiment. The data from the first and second halves can subsequently be used to estimate the effect of the perturbation. The advantages and disadvantages of this method are discussed.

Key words: metapopulations, persistence, acarine predator–prey dynamics, *Tetranychus urticae*, *Phytoseiulus persimilis*.

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INTRODUCTION

There is a large gap between theory and experiments in population dynamics. In a special issue of *Ecology* on realistic models of persistence some years ago, Strong (1990) concluded that there is not much critical experimental evidence for persistence for more than a few systems, and well-designed experiments concerning persistence were long overdue (Hastings, 1990; Reeve, 1990; Taylor, 1990). Since then, the need for ecological time series has increased with the renewed attention for chaotic population dynamics and the lack of evidence for the occurrence of chaos in ecological time series (Godfray and Grenfell, 1993; Hastings *et al.*, 1993; Bascompte and Solé, 1995; Ellner and Turchin, 1995).

One approach to bringing theory and experiments together is to mimic natural systems in theoretical population models by adding as much biological reality as possible. However, this soon leads to complicated models that are impossible to track analytically. Another approach would be to simplify biological systems to make them more like mathematical models. This was our goal when we attempted to establish a persistent experimental predator–prey system, which could be used for experimentation and could be perturbed in order to test theoretical predictions about persistence and dynamics.

There have been several studies of persistence in acarine predator–prey populations. The most well known are those with spider mites and predatory mites in the laboratory by Huffaker (1958) and Huffaker *et al.* (1963). These articles show that considerable complexity has to be introduced into the spatial connection between the local populations to bring about persistence. This was also found by Burnett (1964), who studied populations of stored product mites in the laboratory. Nachman (1981) studied the persistence of predator and prey metapopulations in a greenhouse. He found persistence in three separate greenhouses for 6 months, after which the experiments were terminated. Van de Klashorst and colleagues (Lingeman and van de Klashorst, 1992; van de Klashorst *et al.*, 1992) studied a metapopulation of acarine predators and prey in mini-orchards that persisted in the greenhouse for a period of nearly 2 years. These last two examples showed that acarine predator and prey persist at the spatial scale of a greenhouse. However, greenhouses are too complex an environment to study the causes of this persistence experimentally. Greenhouses are prone to invasions by other pests, which necessitates the use of various control measures that potentially interfere with the populations under study (van de Klashorst *et al.*, 1992). The experiments by Huffaker (1958), Huffaker *et al.* (1963) and Burnett (1964) are better suited to an experimental approach, although the complexity of these systems is still considerable.

We therefore tried to design a laboratory system that would allow predator and prey populations to co-exist and that would permit experimentation on the mechanisms causing persistence. Initially, we started with a simple laboratory experiment with a minimum spatial structure and studied the dynamics of

predators and prey on 90 small bean plants that were placed in a grid. The predators and prey failed to persist in this system. We therefore increased the spatial complexity of the system (see below). This resulted in two replicates that persisted for over 1 year, after which we perturbed the systems to see whether the dynamic properties were altered. In this paper we present an initial time series analysis of the results of this experiment prior to perturbation. Subsequent papers will deal with a spatiotemporal analysis of these data.

MATERIALS AND METHODS

Experimental procedures

In order to minimize the influence of external biotic and abiotic factors, we set up our model system in a climate room with constant temperature ($25 \pm 1°C$) and light. The first experimental arena consisted of one styrofoam platform with a total of 90 small bean plants (*Phaseolus lunatus* cv. Arena). The styrofoam platform had depressions with holes in the centre of the depressions and potted plants were placed in these depressions. The entire platform floated in a tray of approximately 1×2 m, filled with water that provided the plants with permanent access to water through the holes in the platform. The water also served as a barrier to keep the mites on the platform. The plants were 1 week old when introduced into the system, consisted of only two primary leaves and were reared in a greenhouse. All newly developing leaves were pruned during the experiment, so that the plant size remained constant over time. The experiment was started by infesting two plants with one adult female spider mite (*Tetranychus urticae* Koch) on 1 March, 1990, another two plants on 5 March and single plants on 12 and 29 March. These multiple introductions were made in order to introduce temporal asynchrony into the system. Subsequently, 18 adult female predatory mites (*Phytoseiulus persimilis* Athias-Henriot) were released on clean plants over a period of 1 month. The adult female prey and predators were counted twice a week.

The experimental set-up of the second series of experiments is shown in Fig. 1. It consisted of eight styrofoam islands floating in a tray (2×1 m) filled with tap water. The islands had depressions and holes similar to those of the large platform of the first experiment. Each island was connected to each of its two neighbouring islands by two bridges to allow ambulatory dispersal of the predators and prey between the islands (Fig. 1). Because the mites used here have the tendency to walk along structures and rims (Sabelis and Dicke, 1985), the bridges were positioned somewhat lower than the rim of the islands. In this way the bridges were not easily detected by the mites and the probability of mites migrating from one island to the next was reduced. Two replicates of this system, referred to as A and B, were positioned in the same climate room. To reduce the probability of migration from one system to the other, the two systems were placed 1 m apart. Ten bean plants were put on each styrofoam

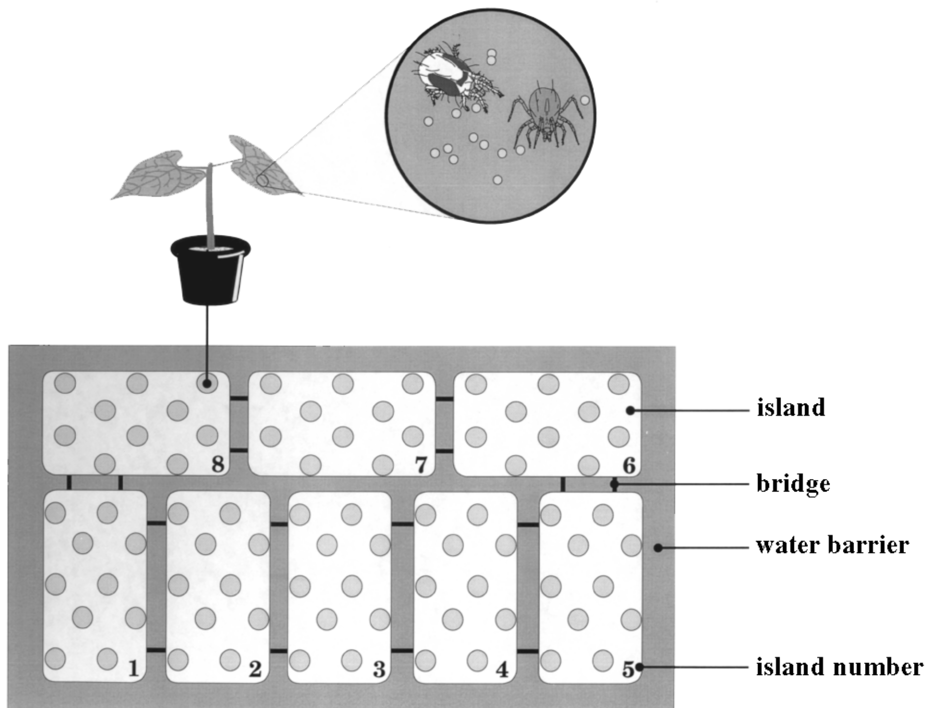

Fig. 1. Set-up of the second metapopulation experiment. Each system consisted of eight islands floating in a 2 × 1 m tray filled with water. The islands were made of styrofoam and had depressions containing potted bean plants. Holes in the centre of the depressions gave the plants access to water. The islands had a rim approximately 6 cm high. Neighbouring islands were connected by cork bridges that were positioned approximately 2 cm below the rim of each island. Ten small bean plants, kept at the two-leaf stage by removing growing tips, were put on each island. At the start of the experiment, phytophagous mites (*T. urticae*) were placed on a few plants. Some weeks later, a few adult predatory mites (*P. persimilis*) were added to the system. Subsequently, all the adult mites on all the plants were counted biweekly. See the text for further details.

island. These plants were again 1 week old. Experience with the first experiment showed that plants reared in a greenhouse may sometimes be infested with other pests such as thrips. Therefore, the plants were reared in a climate room at 25°C. On 8 February 1993, ten adult spider mite prey were put on one plant on islands 3 and 7 in both replicates. After 3 days, four mites had disappeared from one of the plants in system A; they were replaced with new ones. On 18 February, one more plant on island 5 in both replicates was infested with ten adult prey each. On 22 February, three adult female predatory mites were added to the plants on island 3 that were infested with prey on 8 February. Subsequently, no more mites were added to the system. Again, the adult female prey and predators on all the plants were counted twice per week. Migration between the two systems

was checked at times by placing some clean plants in between the two systems. No mites were ever found on these plants, indicating that migration between the two systems did not occur.

The overall plant quality was kept as constant as possible. When the quality of an uninfested plant decreased, as judged by its appearance, it was replaced with a new, 1 week old plant. When a plant was newly infested with spider mites, the spider mite colony was cut out of the leaf with a pair of scissors and was put on a clean, 1 week old plant or the spider mites were moved to such a plant with a fine brush. In this way we tried to minimize the effect of plant age on the population dynamics. Infested plants were not replaced until all the mites had left the plant. Plants had to be free of adult prey for 2 weeks and free of adult predators for 1.5 weeks before we replaced them, thus ensuring that all the eggs and immatures present on the plants had sufficient time to develop into adults and leave the plant.

One year after the start of the second experiment, populations of the prey and predators still persisted in both replicates (based on egg-to-egg developmental rates, 1 year equals approximately 35 and 60 prey and predator generations, respectively). We subsequently perturbed system A, starting from 17 March, 1994. On 9 May, a similar perturbation was applied to both systems. In this paper we restrict ourselves to the results obtained prior to perturbation.

Time series analysis

Data preconditioning: The original data series are discrete time series of biweekly (intervals of 3 or 4 days) data on the population density X of the general form $\{X[t_i]\}$, with $t_i = $ day and $i =$ sample number. For the first series of the second experiment (system A) of both predator and prey the first sample was taken on day 7 so $t_1 = 7$ and the last sample before perturbation on day 393, i.e. $t_{110} = 393$. For the second series (system B) the first sample was taken on day 7 ($t_1 = 7$) and the last on day 447 ($t_{126} = 447$). In order to achieve a reasonable variance homogeneity, the data were log transformed generating series of the form

$$\ln\{1 + X(t_i)\} \tag{1}$$

To reduce the disturbing effects of ‘short-term’ (high-frequency) fluctuations, mainly caused by sampling errors, all the series were filtered through smoothing by threes, generating the series

$$\overline{\ln\{1 + X(m_i)\}}^3 = \frac{\ln\{1 + X(t_i - 1)\} + \ln\{1 + X(t_i)\} + \ln\{1 + X(t_i + 1)\}}{3} \tag{2}$$

(NB: m_i is generally not an integer.)

Subsequently, the time axis was divided into half week (3.5 days) intervals and an uninterrupted series of equidistant data $\{Y_i\}$ was constructed by linear interpolation of the smoothed log-transformed series (Equation 2). Conse-

quently, the length of the two first series is $n = 109$ and of the two second series is $n = 125$.

General statistics and time series analysis: The first step is to estimate any temporal trends in abundance using linear regression and also the sample mean and variance for each series. Estimations of the mean level and trend are needed to adjust the series to the zero mean value and no trend, which are prerequisites to spectral analysis (Lingeman, 1981). The total power represents the integral variance contributions of the trends, periodical components and noise and provides a preliminary impression of the variability of the data.

The autocovariance function (*ACF*) is used to demonstrate the presence of periodicity in the time series. The autocorrelation function (*R*) is formed by dividing the *ACF* by the total variance. Fourier transformation of the *ACF* provides the spectral density function or power spectrum which is used to localize the frequency peaks and/or bands. The estimation procedures of all the covariance and spectral functions mentioned have been extensively described by Lingeman (1981) and Lingeman and van de Klashorst (1992).

RESULTS

Fig. 2 shows the overall dynamics of the first experiment. The interaction between the predator and prey populations ended after 120 days. In the second series, the prey and predators persisted for 393 days in system A and for 447 days in system B, after which the systems were disturbed (Fig. 3). Despite this perturbance, both systems continued to persist until 543 days after the start, after which the experiments were terminated. It seems that the increase in spatial complexity caused by the introduction of the islands connected by bridges resulted in persistence of the system (cf. Figs 2 and 3).

Despite the equal treatment and equal initial conditions of both systems in the second experiment, the dynamics of the two systems differed right from the beginning. Both systems showed rather erratic dynamics: system A showed some evidence for the existence of cycles, whereas no sign of such cycles could be detected in system B. Table 1 shows the general statistics of the transformed and smoothed time series. The mean numbers of predators and prey were approximately equal in both series, while the variance was somewhat but not significantly higher in the second series. There was no sign of a trend through time in the first series, whereas there was a clear trend in the second series; the mean log numbers of the prey decreased, whereas the mean log numbers of the predators increased over time (Table 1 and Fig. 4).

To investigate the differences between the two replicates in more detail, we compared the data sets of both systems using time series analysis. The data from both series were scaled to a mean value of zero and the trend was removed from the second series. Both resulting data sets still differed considerably; the prey

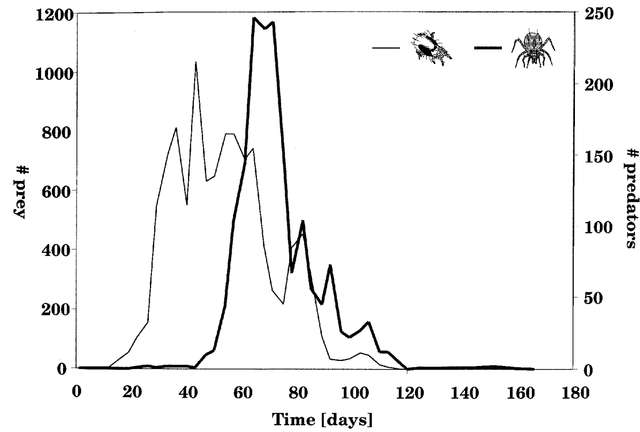

Fig. 2. Numbers of prey (thin black line) and predators (thick grey line) in the first experiment.

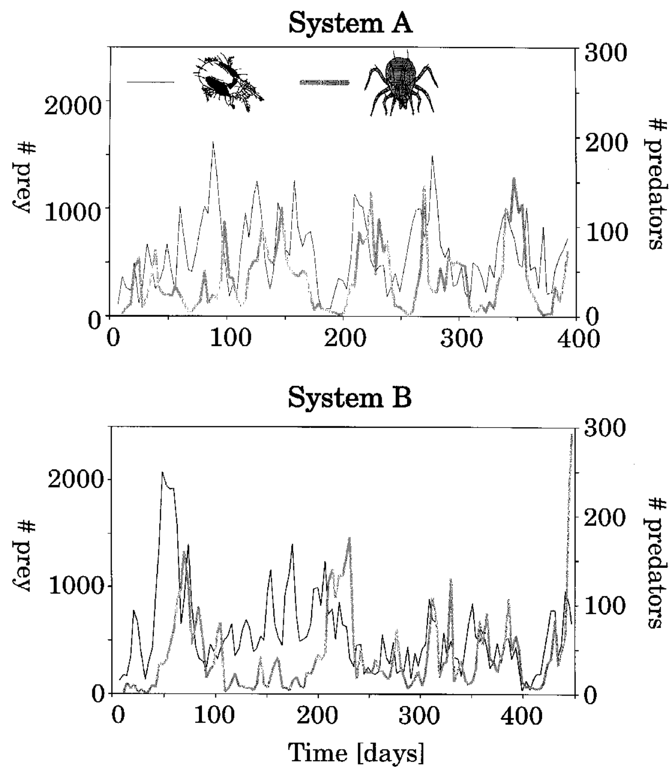

Fig. 3. Numbers of prey (thin line) and predators (thick grey line) through time in both metapopulation systems of the second experiment.

TABLE 1

General statistics of the two time series of the second experiment

	System A ($n = 109$)		System B ($n = 125$)	
	Prey	Predator	Prey	Predator
Mean	6.201	3.323	6.140	3.333
Variance	0.305	0.841	0.362	0.865
Slope	0.0003	− 0.0004	− 0.0065	0.0069
Intercept	6.185	3.345	6.548	2.900
p	0.87	0.89	< 0.001	0.003

The computations were performed on the log-transformed numbers (see the text).

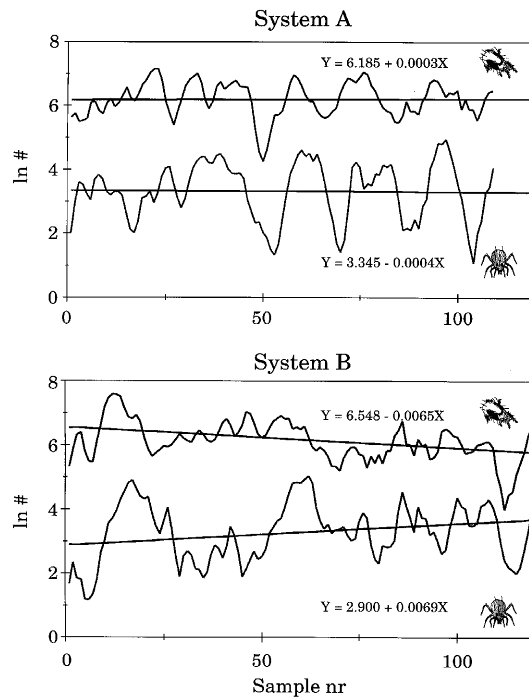

Fig. 4. Smoothed time series of both systems. The top lines show the data for the prey and the bottom lines that of the predators, both as a function of the sample number (the samples are numbered in chronological order). Straight lines indicate the regression lines of the data through time. Regression equations are given for each line. See Materials and methods for the smoothing procedure.

and predator populations showed some periodicity in system A, whereas there was no sign of a periodic component in system B (Fig. 5). This was further confirmed by the *ACF*s of both systems. Both the prey and predator populations of system A showed a clear periodicity with a lag of 17 sample units (8.5 weeks), whereas system B did not show this periodicity (Fig. 6). The log power spectra again showed a distinct dominant frequency of six cycles per year (c.p.y.) for system A (each cycle takes approximately 8.5 weeks), whereas the dominant frequency in system B was approximately 2.5 c.p.y. (a period of 20.8 weeks) (Fig. 7).

DISCUSSION

A comparison of the two experiments suggests that the persistence in both replicates of the second experiment is caused by the increased spatial complexity of the system. This is in agreement with the results of Huffaker (1958), Huffaker *et al*. (1963) and Burnett (1964). The systems of the second experiment consisted of fewer plants than the first experiment, but they were distributed over eight islands connected by a few bridges. The populations in this system did show an overall persistence, but no persistence of the predators and prey was observed on any of the separate islands, suggesting that the

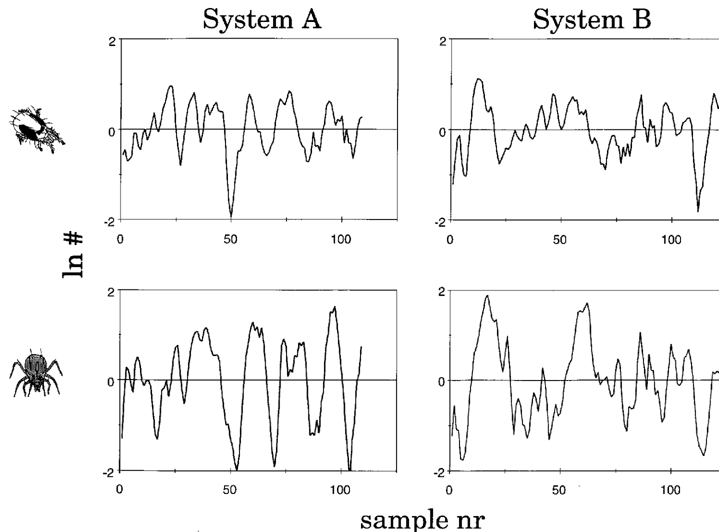

Fig. 5. Time series of both systems in the second experiment, with the series scaled to zero and trends removed. The data for the prey (top graphs) and predators (bottom graphs) for systems A (left) and B (right) are shown. See Materials and methods for the scaling procedure.

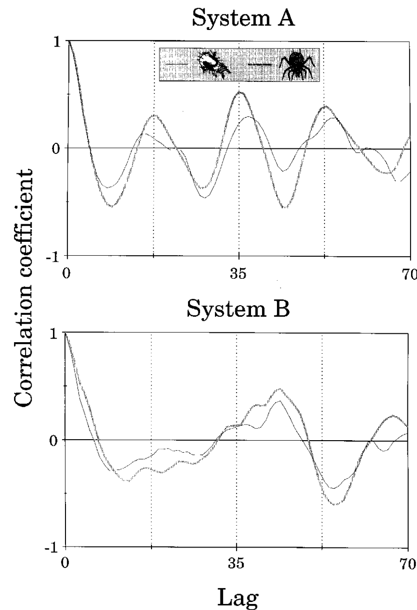

Fig. 6. Autocorrelation function for both systems. The correlation coefficient is shown as a function of the time lag is shown. The top graph shows the data for system A (thin line, prey and thick grey line, predators) and the bottom graph is for system B. See Materials and methods for the procedure of the time series analysis.

persistence is caused by limited migration between the eight asynchronously cycling unstable subsystems. The length of the predator–prey cycles in the first system of the second experiment was approximately 60 days, whereas the length of the single predator–prey cycle in the first experiment lasted approximately 110 days (Fig. 2). However, there were hardly any predators present in the first period of the first experiment. This is probably due to the method of introduction used: the predators were randomly placed on plants without prey and the probability that they found a prey population on another plant was small. As a result many of the predators introduced died without finding any prey. When this first period of approximately 50 days is disregarded, the cycle length again is approximately 60 days (Fig. 2).

In our experiments, the dispersal of both predators and prey was potentially limited by the presence of islands connected by bridges. Sabelis *et al.* (1991) studied the effect of prey and predator dispersal on the dynamics of a simple Lotka–Volterra metapopulation model inspired by acarine predator–prey systems like the one studied here. They found that the dispersal of prey had a stabilizing effect on the dynamics, whereas the dispersal of predators had a destabilizing effect. However, their model contained no explicit spatial

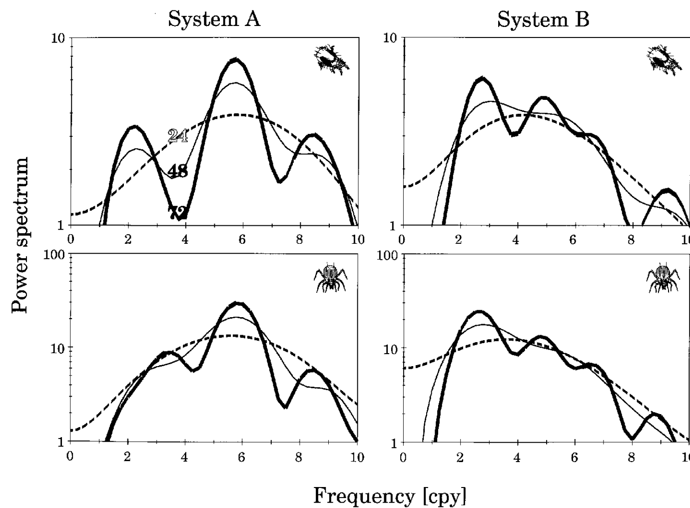

Fig. 7. Power spectra of both time series. The log power spectra per frequency for three spectral windows ($M = 24$, 48 and 72) are shown. The left two graphs are for system A (top, prey and bottom, predator) and the right two graphs are for system B. See Materials and methods for the procedure of the time series analysis.

structure, making a comparison between the two studies difficult. Nachman (1987a,b) described a stochastic simulation model with spatial structure for the dynamics of *P. persimilis* and *T. urticae* on cucumber in a greenhouse. He found that his system was quite robust to changes in the rates of migration and even low rates of dispersal were sufficient for persistence. Higher rates of dispersal of the predators resulted in a decreased persistence. Nachman's (1987a,b) model can produce dynamical patterns that closely resemble our experimental results (G. Nachman, personal communication). However, a phase diagram of his system showed cycles (phase-forgetting quasi-cycles; Nachman 1987b), whereas our systems do not show this (Fig. 8). The dynamics within subunits of the systems are unstable in both our and Nachman's (1987a,b) systems. In our experiments, interactions on a single plant ended either because the plant was overexploited or because the prey were exterminated by predators. Only in the second case, that of prey extermination, would the phase diagram of local dynamics (i.e. dynamics on one plant) show one cycle, starting with a newly arrived prey mite and ending with zero prey and predators. A phase diagram of the entire system then consists of a summation of all the local phase diagrams, some of which show cycles while others only show increases and decreases of prey numbers. For this reason, it seems logical that no cyclic behaviour was found in the phase diagram, where the time dimension is excluded, although cycles were found in the numbers of predators and prey over time in system A. In Nachman's (1987) system, the plants died very infrequently from

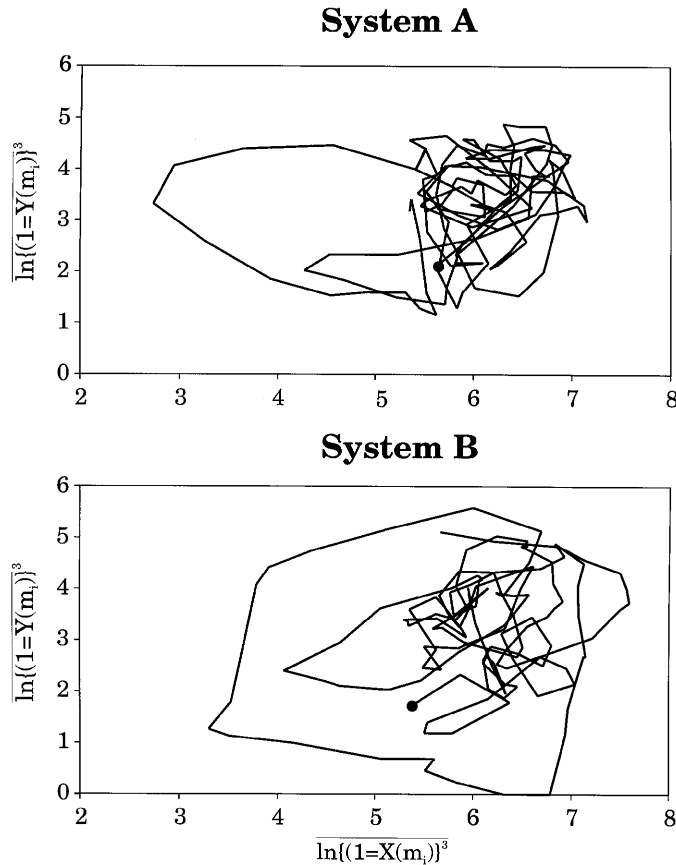

Fig. 8. Phase diagram of both time series. The smoothed time series of the prey (x-axis) and predators (y-axis) are shown. Dots indicate the start of the experiment. See Materials and methods for the smoothing procedure.

overexploitation; hence, local interactions usually show a cycle in the phase plane. As a result, the overall dynamics still do show cycles.

Despite efforts to keep the initial conditions as equal as possible for both replicates, we were unable to create two replicate metapopulation experiments with the same type of dynamics. The resulting time series from one system show a clear periodicity with a period of 8.5 weeks, whereas the time series of the other system have a dominant period of 20.8 weeks (Fig. 7). Moreover, both the prey and predator data series of system B show a significant trend through time and this trend is absent in system A. The differences may be caused by stochasticity in the initial phase of the experiment, and could be indicative of the presence of a chaotic attractor.

The measurement of population dynamics under laboratory conditions has a rich tradition (Nicholson, 1954, 1957; Udita, 1957; Huffaker, 1958; Burnett,

1964; Salt, 1967; Tsuchiya *et al*., 1972; Jost *et al*., 1973; Luckinbill, 1973; Veilleux, 1979). Most of these time series concern the dynamics of well-mixed populations without an explicit spatial structure. Only Huffaker (1958), Huffaker *et al*. (1963) and Burnett (1964) studied systems that can be considered as consisting of local populations connected through dispersal; all these studies concern acarine predator–prey systems. Huffaker (1958) presented data of one persistent acarine predator–prey system with a complex spatial structure. Huffaker *et al*. (1963) showed results of one spatially structured persistent prey system, along with two replicate experiments with predators and prey. One of these latter two systems persisted for a period of 70 weeks, after which the predators disappeared. In the other replicate the predators disappeared after 23 weeks. The quality of the prey food was not constant during both replicates and a pathogen killed many prey during the last phase of the first replicate. Three other experiments with more food available to the prey showed short periods of existence, i.e. one predator–prey cycle as in our first experiment. Burnett's (1964) research also showed the data of several experiments. As in our case and in Huffaker's (1958) replicates, Burnett's (1964) data showed that replicate series may differ considerably. However, some of his replicates were invaded by another prey species, and this probably changed the dynamics of the predators and prey. Hence, Huffaker (1958), Huffaker *et al*. (1963) and Burnett (1964) all found differences between the replicates of their experiments, but this could have been caused by various external factors such as an infestation by pathogens or other prey species or the quality of the prey food. Differences between our replicates due to external conditions were much less likely to occur, since both experiments were performed at exactly the same time, with the same quality of prey food and under the same environmental conditions.

Holyoak and Lawler (1996a,b) recently presented a series of elegant experiments showing an increased persistence of an otherwise unstable predator–prey interaction due to an increase in the complexity of their experimental set-up. They performed three replicates of the experiments with two different sizes of spatially subdivided containers and the dynamics of each replicate with a similar size showed the same overall densities of prey and predators (Holyoak and Lawler, 1996b), as do the two replicates of our persisting system (Table 1). Holyoak and Lawler (1996) did not specifically test for periodicity in the overall densities of the prey and predators in their subdivided containers, but a visual inspection of their results shows quite constant predator densities, whereas the prey densities show larger fluctuations. If any periodicity was present in these data, the frequency of the cycles would probably have varied from replicate to replicate (Holyoak and Lawler, 1996b, Fig. 5). Holyoak and Lawler (1996b) stated that few studies have provided data that demonstrate metapopulation dynamics. The evidence needed to prove that persistence is caused by a metapopulation structure is that (1) the predator and prey cannot persist in a local patch when it cannot be reached by dispersers

(note that this is a combination of two of the points mentioned by Holyoak and Lawler, 1996b, and (2) the predator and prey populations cannot persist in an undivided habitat of equal size as the subdivided habitat (Holyoak and Lawler, 1996). The data presented here meet both criteria, so we can conclude that this study is yet another example of the persistence of a locally unstable predator–prey system through a metapopulation structure. Another study that appears to meet these criteria is that of Huffaker (1958), but a complicating factor in those experiments was the varying starting conditions used for the different experiments.

Our experiments clearly show that replicate metapopulation experiments, even under controlled conditions in the laboratory, exhibit different dynamics. As a consequence, more replicates need to be performed to reveal the range of dynamic patterns. This makes perturbation experiments with replicated controls very difficult to perform. Due to an increase in the occurrence of random fluctuations, attempts to perform replicate experiments will probably prove even more difficult under more natural conditions, such as in greenhouses or outdoors. In our opinion, it is therefore undesirable to design replicate experiments where one of the two replicates serves as a control for the other, unless stable dynamics are expected. An exception to this might be systems that show stable dynamics with only minor effects of random fluctuations.

An alternative approach would be to run long-term experiments where the system is left undisturbed initially. During this time, the resulting time series should be checked for trends and constant periodicity and perturbations should be started well beyond the possible initial transient periods. Subsequently, the effects of the perturbations can be studied by comparing the first half of the data set with the second half. In other words, the first half of the experiment serves as a control for the perturbation effects in the second half. Rasmussen *et al.* (1993) discussed this method, which is called intervention analysis. They stressed the importance of replications, because it is the only way to reduce the probability of detecting spurious treatment effects in a readily quantifiable manner. A prerequisite for this is that the replicates should be comparable before the perturbation, which was not the case in our study.

An obvious disadvantage of this approach is that the biological system may change as a result of selection during long time series, resulting in other dynamic properties. Hence, the effects of experimental manipulation may be indistinguishable from the effects of evolutionary changes. A way to circumvent the occurrence of changes would be to start with genetically homogeneous populations by using the offspring of inbred isofemale lines for both the predators and prey. When it is impossible to work with isofemale lines, one way of checking for the occurrence of evolutionary changes would be to study repeatedly the behaviour and life history of the species involved. Any change in these properties would be the result of selection due to experimental conditions or of drift due to the relaxation of the selection pressure.

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