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The role of dispersal in predator–prey metapopulation dynamics

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Summary

1. We report the role of dispersal in the metapopulation dynamics of a protist predator–prey pair, the predaceous ciliate *Didinium nasutum* Müller feeding on the bacterivorous ciliate *Colpidium* cf. *striatum* Stokes. In previous work we showed that this extinction-prone pair persisted as metapopulations in subdivided habitats.
2. An experiment assessed the effects of habitat subdivision on persistence and dynamics. Undivided habitats were 270 or 750 mL in volume, and subdivided habitats (arrays) were sets of nine or 25 linked 30 mL bottles (270 or 750 mL total volume), each replicated three times. Undivided microcosms allowed maximum dispersal, whereas subdivision reduced dispersal. Within arrays, bottles with more connecting tubes allowed more dispersal. Nine and 25 bottle arrays also differed in the mean number of connections per bottle. The effects of dispersal on predator–prey dynamics were tested by comparing subdivided vs. undivided microcosms, bottles with different numbers of connecting tubes, and nine vs. 25 bottle arrays.
3. We tested the following predictions from metapopulation theory. (i) Predator and prey persistence and predator abundance will be greatest at intermediate dispersal rates. (ii) Prey abundance, local population variability and asynchrony in population fluctuations will be greatest at low dispersal rates. (iii) Predator:prey ratios will be greatest at high dispersal rates.
4. Predictions were confirmed, except for the following. (i) Two measures of synchrony differed in whether they showed the expected pattern. Spatial synchrony (estimated via correlation of densities among patches within sampling dates) showed high variance and did not vary with dispersal rates. However, spatial variability (CV of density across adjacent pairs of linked bottles), showed the predicted decrease with increased dispersal. (ii) Evidence that dispersal increases predator:prey ratios was inconclusive. Predator:prey ratios were lower in undivided 750 mL microcosms than in 750 mL arrays, possibly because predators over-exploited prey in undivided microcosms, so that both became scarce. Conversely, within arrays, predator:prey ratios were greatest in bottles that allowed the most dispersal, as predicted.
5. This work generally confirms the predicted effects of dispersal on predator–prey metapopulation dynamics. It also demonstrates the need for models to include more realism, e.g. the possibility of over-exploitation with very high dispersal.

Key-words: persistence, predation, Protista, rescue-effects, subdivision.

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Introduction

In theory, predators and prey with extinction-prone local populations can persist at a regional (metapopulation) scale if populations are linked by dispersal (reviews Hanski 1991; Taylor 1990, 1991; Harrison & Taylor 1995). In an archetypal metapopulation, regional persistence occurs because dispersal balances local extinctions with recolonizations (Levins 1970). Dispersal could also prevent local extinctions entirely by augmenting local population size; this has been termed 'rescue effects' by Brown & Kodric-Brown (1977). The amount of dispersal among populations is the key to metapopulation persistence: low colonization rates will not

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balance extinctions, while very high dispersal may synchronize populations so that all go extinct simultaneously. Models of predator–prey metapopulations predict that dispersal will also affect other aspects of local and regional dynamics, such as the relative abundances of predators and prey, and the amplitude of population fluctuations (reviewed below). In this paper we test the effects of different levels of dispersal on local and regional predator–prey dynamics.

A number of models of predator–prey metapopulation dynamics consider both dynamics within local populations and in the entire metapopulation. Two models address host–parasitoid dynamics (Reeve 1988; Hassell, Comins & May 1991), two are general models of predator–prey interactions (Zeigler 1977; Crowley 1981) and one considers a tritrophic (plant, herbivore and predator) interaction in greenhouse mites (Nachman 1987a,b). Much of our knowledge of predator–prey metapopulation dynamics comes from such models (reviews Taylor 1990, 1991). Surprisingly, dispersal has similar effects on dynamics in all of these models (described below), indicating that the effects are likely to be general. The influence of dispersal on predator–prey metapopulation dynamics has generally not been tested because many of the relevant experiments were conducted before theories of predator–prey metapopulation dynamics existed (e.g. Huffaker 1958; Huffaker, Shea & Herman 1963; Pimentel, Nagel & Madden 1963; Maly 1978; but see Nachman 1987a,b, 1991 for an exception). Data from real organisms should either show the predicted effects of dispersal on metapopulation dynamics, or aid us in identifying reasons why observed and predicted dynamics differ.

The effect of dispersal on predator–prey metapopulations can be understood if we consider the effects of low and high dispersal rates on dynamics (after Reeve 1988). The following ideas are based on models which assume that predators and prey have equal dispersal rates, and that the interaction cannot persist in isolated patches. We describe the predictions of the models here and reference specific models in a numbered summary below; predictions are summarized qualitatively in Fig. 1.

At extremely low dispersal rates, new patches are not colonized often enough to balance extinctions (cross-hatched area of Fig. 1). The rate of colonization of new patches by predators and prey will increase as dispersal rates rise.

At low dispersal rates (but high enough that colonization balances extinction), prey could temporarily escape in space from predators. Prey that arrive at a vacant patch before predators are likely to become abundant before predators colonise. This potentially makes prey most abundant at low dispersal rates (Fig. 1a). Large-amplitude fluctuations in predator and prey abundances are also characteristic of low dispersal rates (Fig. 1b). This is because predators that colonize patches where prey are abundant will show

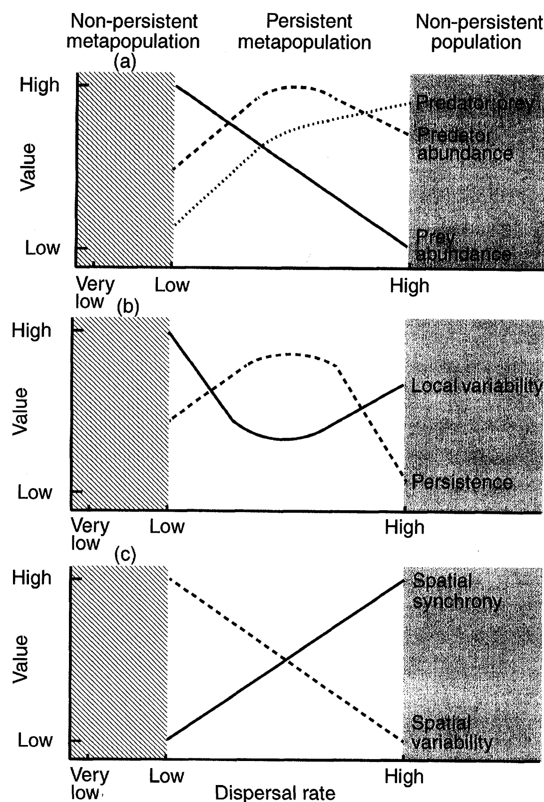

Fig. 1. Predicted effects of dispersal rates on predator–prey metapopulation dynamics. The predator–prey pair is assumed to be extinction-prone in local populations, and the species are assumed to have similar dispersal rates. At the lowest dispersal rates (cross-hatched area) long-term persistence of the pair is impossible because recolonizations do not balance local extinctions. At the highest dispersal rates (shaded area) the entire system behaves as a single large population, in which the pair cannot persist. The pair can persist as predator and prey metapopulations between these extremes. (a) Average prey and predator abundances and predator:prey ratio. (b) Average within-patch population variability (local variability) and persistence time; for persistence time, the line represents both local and regional persistence. (c) Predicted synchrony in fluctuations in prey or predator abundance in patches at a given distance apart, plus a surrogate measure of synchrony termed spatial variability. Spatial variability is the temporal variability in densities (of predators or prey) measured among a fixed number of patches. Graphs have been drawn to show the relative positions of maxima and minima in dynamical measures, and the precise slopes and shapes of curves are arbitrary.

a large numerical response. Subsequent 'crashes' and local extinctions are also likely at low dispersal rates, because both species are likely to remain in the same patch, and densities are unlikely to be augmented by immigration. Population dynamics should be asynchronous among patches, because low dispersal rates cause patches to be colonized at different times and dispersal is unlikely to equalise densities across patches (Fig. 1c).

As dispersal rates increase to intermediate levels, the likelihood of dispersal from high to low density patches (rescue effects) will increase up to the point where asynchrony starts to break down because patches

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are colonized at similar times and dispersal equalizes density across patches. Rescue effects reduce the chance of local extinction of the species concerned, and damp the size of fluctuations in local density by augmenting densities that are low. Thus, local variability should be lower, and synchrony higher, at intermediate dispersal rates than at low dispersal rates (Fig. 1b). Average predator abundance should be greater because the predators find more patches with prey, while average prey abundance is lower because there are fewer patches without predators (Fig. 1a).

When dispersal rates are high, predators reach all patches and over-exploit prey, reducing both predator and prey abundance. Predators should therefore be most abundant globally at intermediate dispersal rates (Fig. 1a). Nachman (1987b) predicts that predators will decline less rapidly than prey as dispersal rates increase, causing the predator:prey ratio to rise at higher dispersal rates (Fig. 1a). At very high dispersal rates, metapopulation dynamics break down because dispersal synchronizes all local populations, precluding rescue effects and making simultaneous extinction of all subpopulations likely (shaded portion of Fig. 1).

From the above we can distill the following predictions.

1. Both local and regional persistence of predators and prey is greatest at intermediate dispersal rates of both species (Zeigler 1977; Crowley 1981; Nachman 1987b; Reeve 1988; Hassell, Comins & May 1991; Comins, Hassell & May 1992).

2. Prey densities will be greatest at low dispersal rates, while the predator will be most abundant at intermediate dispersal rates (Zeigler 1977; Nachman 1987b; Reeve 1988).

3. Predator–prey ratios will be greatest at high dispersal rates, because prey decline more rapidly than predators as dispersal rates rise (Nachman 1987b).

4. The size of fluctuations in local predator and prey density is greatest at low dispersal rates of both species (Reeve 1988).

5. Asynchrony in fluctuations among local populations is greatest at low dispersal rates (Zeigler 1977; Crowley 1981; Nachman 1991).

In a separate paper we reported that a protist predator–prey pair persisted via metapopulation dynamics in subdivided microcosms, but went extinct in undivided microcosms (Holyoak & Lawler, in press). The pair were the predaceous ciliate *Didinium nasutum* Müller feeding on the bacterivorous ciliate *Colpidium* cf. *striatum* Stokes. Predators and prey persisted for 130 days in arrays of 25 linked bottles (≈602 prey and 437 predator generations), whereas predators persisted for a mean of only 60 days in undivided microcosms of equivalent total volume (Holyoak & Lawler, in press). Predators and prey showed metapopulation dynamics in the arrays; both species had low dispersal rates, showed only partially synchronous population fluctuations in adjacent patches, and persisted despite

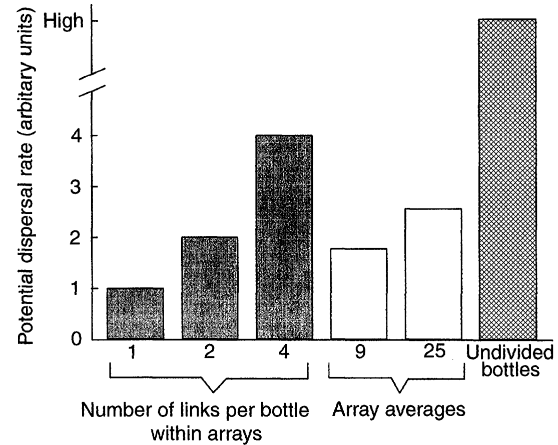

Fig. 2. Relative levels of dispersal for various types of containers used in a microcosm study of the role of dispersal in predator–prey dynamics. Shaded bars represent the amount of dispersal in bottles with 1, 2, or 4 links to other bottles within arrays. Open bars show the expected difference in dispersal within nine-bottle arrays vs. 25-bottle arrays; the former had fewer connections per bottle. The hatched bar shows high dispersal within undivided volumes.

extinction-prone local dynamics. In prey, local extinctions and recolonizations were frequent, whereas predators rarely went locally extinct because rescue effects augmented local population density.

The study provided a detailed record of spatiotemporal dynamics that can be used to test differences in population dynamics caused by dispersal in undivided microcosms and subdivided microcosms. Undivided microcosms allowed maximum dispersal, whereas subdivision reduced dispersal (Fig. 2). Within subdivided arrays, the dispersal rate is expected to rise in direct proportion to the number of tubes connecting bottles (Fig. 2). We compared predator–prey dynamics with different dispersal rates by comparing dynamics in different kinds of microcosms and in bottles with different numbers of tubes within arrays. We are cautious to rule out confounding effects of microcosm volume when comparing dynamics in microcosms of different total volume.

Materials and methods

The predator *D. nasutum* and bacterivorous prey *C. striatum* were supported on a mixed bacterial suspension in semi-continuous batch culture using aqueous nutrient medium made from Protozoan Pellets™ (Carolina Biological Supply Co.). Each 30 mL volume also contained a millet seed that provided a slow release of nutrients. Containers were chosen so as to keep air-surface to volume ratio constant. Culture vessels were either spatially continuous glass containers (270 or 750 mL), or subdivided microcosms ('arrays') constructed by linking nine or 25 polypropylene bottles of 30 mL volume, giving total volumes of 270 and 750 mL. The layout of arrays is shown in Fig. 3. There were three replicates of each

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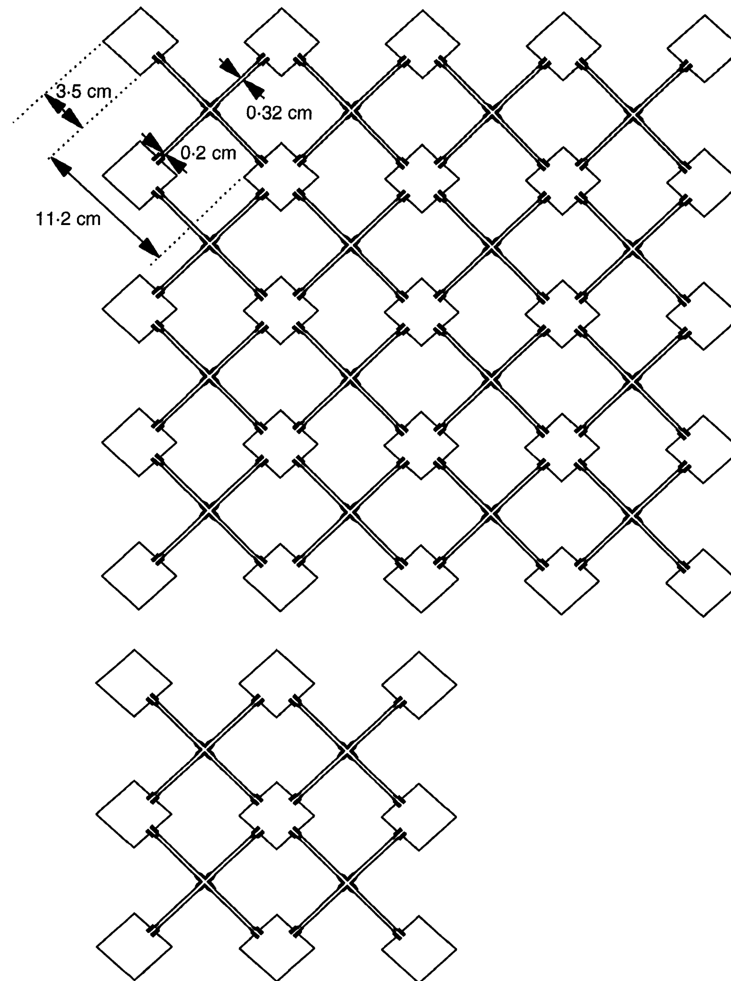

Fig. 3. Plan view showing both 25-bottle and 9-bottle subdivided microcosms. Diameter of every tube varied between 0·2 and 0·32 cm because of the use of connectors.

volume in subdivided and spatially continuous treatments. Microcosms were kept at room temperature (22 ± 2 °C).

Microcosms contained bacterized protozoan pellet medium. One day after the microcosms were filled with medium, ≈56 *C. striatum* from a stock culture were added to each 30 mL volume. After another day, ≈27 *D. nasutum* were added to a corner bottle of each array and to a corner of each undivided container. This created an initial difference in predator:prey ratios between different volumes, but this difference could not explain greater persistence times in subdivided microcosms than undivided microcosms of the same volume (Holyoak & Lawler, in press).

A 1·8 mL sample was taken weekly from each 30 mL (all array bottles and a sample per 30 mL from undivided microcosms) up to day 54 and at 2-day intervals between days 54 and 102 to collect a detailed record of spatio-temporal dynamics. After day 102 samples were taken at 2-day intervals, but were only counted on days 110, 120 and 130, when the experiment was halted. In quantifying dynamics, unless otherwise stated, we used series of abundances from 20 samples at 2-day intervals starting on day 54. Prior to removing samples, contents of containers and individual array bottles were thoroughly mixed with a Pasteur pipette. Samples were replaced with fresh sterile medium.

C. striatum and *D. nasutum* were counted using a binocular microscope to census a 3-drop subsample taken from the 1·8 mL sample. If <3 individuals were present the rest of the sample was censused. In preliminary experiments this procedure gave a coefficient of variation between samples of 0·16 for predators and 0·09 for prey ($n = 90$). All counts were transformed to numbers of cells per mL.

We were not able to confirm local extinctions of predators or prey within subdivided microcosms without disrupting the experiment. To estimate the frequency of local extinctions we therefore compared the frequency of zero density values within bottles of arrays with dynamics within isolated 30 mL bottles where extinctions were confirmed. Isolated 30 mL bottles were controls in an experiment to test the effect of immigration on local dynamics (Holyoak & Lawler, in press). This experiment was set up under identical conditions to the main experiment, except that initial numbers added were ≈ 12 *C. striatum* and exactly 4

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D. nasutum (per 30 mL for both species), and predators were added 2 days after prey. The experiment was sampled at 2-day intervals, as in the previous experiment. If a species was absent in a sample, the entire 30 mL was checked under the microscope to confirm absence, and this was repeated for five additional sampling dates. We then calculated the proportion of zero sample densities that represented real extinctions.

C. striatum shows logistic growth in the absence of *D. nasutum*, and has never been observed to drive its bacterial prey extinct (Morin & Lawler 1995). We therefore treat *D. nasutum* and *C. striatum* as a simple predator and prey system as previous authors have done with *D. nasutum* and *Paramecium* (Gause 1934; Luckinbill 1973, 1974, 1979; Salt 1974, 1975; Luckinbill & Fenton 1978; Maly 1978; Hewett 1980, 1987).

Our paper is based on two reasonable assumptions: (i) more dispersal of both species occurred in undivided microcosms than in arrays because the former had no internal barriers, and (ii) the amount of dispersal within arrays was a function of the number of connecting tubes. Array bottles had 1, 2 or 4 connecting tubes (Fig. 3). We did not quantify dispersal rates in the undivided microcosms, but we did measure dispersal rates of predators and prey between two bottles linked by a single tube (Holyoak & Lawler, in press).

We calculated persistence times, average density of each species, predator:prey ratio, and local variability (the coefficient of variation, or CV of density across time within bottles). The reasons for using CVs to quantify temporal population variability are reviewed by Gaston & McArdle (1994). We also calculated spatial variability and spatial synchrony for predators and prey; these two measures are defined below.

'Spatial synchrony' was calculated by finding the correlation in densities among all bottles within dates, using the series of samples at 2-day intervals. We used lag-zero cross-correlations (Hanski & Woiwod 1993) and assessed how cross-correlation changed with the distance between bottles within subdivided microcosms. Lower correlation reflects lower synchrony. To avoid making comparisons between statistical analyses that were conducted with different sample sizes we held the number of bottles at nine, the size of the smaller arrays. In the larger 25 bottle arrays we considered only a 3×3 block of bottles in one corner of the array.

'Spatial variability' was the coefficient of variation of density in pairs of adjacent bottles across time, calculated using all the density values from both 20 sample time series. Greater spatial variability shows that there is greater asynchrony in fluctuations in local population size, so that there is more chance for recolonisations and rescue effects. To judge whether dispersal affected spatial variability, we held the number of connections in the first bottle constant (at four) and varied the number of connecting tubes which the second bottle possessed. Spatial variability is a useful surrogate measure of asynchrony, and is less reliant on sample size than spatial synchrony.

We made three kinds of comparisons: (i) Regional dynamics in subdivided arrays (using density averaged across all bottles) vs. those in undivided microcosms of equivalent total volume. Dynamics compared were persistence time, mean density and predator:prey ratios. (ii) Bottles within subdivided arrays which had different numbers of connecting tubes. Dynamics compared were number of zero density values, mean density, CV of density through time, and spatial variability. (3) Nine vs. 25 bottle arrays. Nine bottle arrays had an average of 1·78 tubes per bottle and 25 bottle arrays had 2·56 tubes per bottle (Figs 2 & 3). Statistics compared were number of zero density values, mean density, spatial variability, and spatial synchrony. The comparison of nine and 25 bottle arrays is potentially confounded by differences in volume. We therefore used data from undivided microcosms of equivalent total volume to the arrays to check whether or not differences between nine and 25 bottle arrays could be explained by differences in volume.

Prior to conducting either Student's *t*-tests or ANOVAs we checked that the distribution of the variable being tested did not differ (at $0{\cdot}1 < P < 0{\cdot}9$) from normality using a χ^2-test. We applied Bartlett's test for homogeneity of variances and only carried out parametric ANOVAs if variances were homogeneous between treatments. Distributions were also checked by eye and we transformed response variables as appropriate, leading us to use: Ln(density + 1), Ln(persistence), Ln(CV of within-bottle density), which is local variability, and Ln(CV of density across pairs of adjacent bottles in arrays), which is spatial variability. We used sequential Bonferroni tests to identify treatments that differed in ANOVAs. Differences were termed significant at $P \leqslant 0{\cdot}05$.

We tried to eliminate confounding factors that could explain differences in persistence or dynamics between undivided microcosms and arrays. We kept air surface:volume ratios constant across containers, provided volume controls for each array size, and held initial predator:prey ratios constant within volumes. General conditions for growth of protists was similar in divided and undivided containers. A side experiment showed that *C. striatum* grew at the same rate and reached the same densities in medium sampled from undivided and subdivided arrays on day 94 of the experiment (unpublished data). Predators reintroduced into undivided microcosms (after initial predator extinctions) were able to increase in numbers and survive for several months (unpublished data). We cannot rule out the unlikely possibility that bacterial dynamics differed between subdivided and undivided microcosms; however, this would probably have been reflected as a difference in the growth rate of *Colpidium* in the medium from divided vs. undivided arrays. Differences in dynamics were unlikely to result

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from predators or prey behaving differently in connecting tubes; neither predators (Berger 1980) or prey aggregated on surfaces nor did they appear to aggregate in or avoid tubes.

Results

PERSISTENCE

To judge how dispersal affected persistence, we compared regional persistence in entire subdivided arrays vs. undivided microcosms, and also estimated the frequency of local extinctions in individual array bottles (patches) with different numbers of connecting tubes. Overall there was good evidence that predator and prey extinctions were less frequent at intermediate levels of dispersal:

1. Undivided 270 and 750 mL volumes allowed the most dispersal, and persistence times of predators in these were shorter than their regional persistence times in arrays. Average persistence times for the undivided 270 and 750 mL microcosms were 81 and 60 days, respectively (Table 1), but neither predators or prey went extinct regionally in arrays before the experiment was halted at day 130 ($P < 0{\cdot}05$, Student's t-test on ln-transformed persistence times; see also Holyoak & Lawler, in press). Prey persisted regionally in all microcosms of 270 and 750 mL.

2. Within arrays, we compared the frequency of zero densities in bottles that had different numbers of connecting tubes. In previous work, we found that 35% of single recorded zero densities in samples represented real extinctions for prey, and 49% of zero values were extinctions for predators (Holyoak & Lawler, in press). The frequency of zero density values was greater (using sequential Bonferroni tests) in bottles with one connection than in those with two or four connections in nine bottle arrays for prey, and in 25 bottles arrays for predators (Fig. 4a, d). Other differences were non-significant in one-way ANOVAs (Fig. 4). These comparisons show that local persistence was more likely in bottles with more connections, so the level of dispersal at which local persistence is most likely is equal to or greater than the maximum dispersal rate (4 connections) in subdivided microcosms.

3. Local persistence was greater in 25 bottle arrays than in nine bottle arrays. Since the former have a greater number of connecting tubes per bottle, this result is consistent with persistence being greatest at or above the maximum dispersal rates in subdivided arrays. We used a three-way ANOVA to compare Ln(number of zero densities) between species, microcosm types and levels of connectivity. The difference between nine and 25 bottle arrays was significant ($F_{1,32} = 4{\cdot}67$, $P < 0{\cdot}05$), and sequential Bonferroni tests showed that the difference between nine and 25 bottle arrays was due to differences between bottles with one connecting tube for prey (compare Fig. 4a, c) and for bottles with one or two connecting tubes for predators (Fig. 4b, d). Zero densities and hence local extinctions were more frequent in nine bottle arrays than in 25 bottle arrays for both predators and prey. Protists did not go extinct sooner in undivided microcosms of 270 mL than in 750 mL volumes, which indicates that the difference between subdivided microcosms was not due to microcosm volume.

ABUNDANCE

Predators and prey were more abundant in 25 bottle arrays than in the equivalent 750 mL undivided volume (Table 1). This shows that predators and prey were most abundant at a dispersal rate which is less than

Table 1. Statistics from time-series of densities from microcosms. In subdivided arrays, the values of mean density and predator:prey ratios represent average dynamics in entire arrays; therefore, a single time-series was constructed for each replicate by averaging densities in all bottles. Neither lumped average Ln(density + 1) values or Ln(persistence times) differed (at $0{\cdot}1 < P < 0{\cdot}9$) from a normal distribution in χ^2-tests; one-tailed Student's t-tests (with 4 degrees of freedom) were conducted on transformed values. NS indicates non-significance ($P \gg 0{\cdot}05$)

		Undivided microcosms		Subdivided arrays 9 bottle	Subdivided arrays 25 bottle	t for subdivided vs. undivided microcosms	
Statistic	Species	270 mL	750 mL	(270 mL)	(750 mL)	270 mL	750 mL
Persistence time (days)	Predator	81· ± 5·1	59·7 ± 20·3	130*	130*	2·46 $P < 0{\cdot}05$	2·15 $P < 0{\cdot}05$
Mean ln (density + 1)	Prey	1·27 ± 0·86	0·46 ± 0·04	0·96 ± 0·14	0·92 ± 0·10	0·36 NS	4·27 $P < 0{\cdot}01$
	Predator	0·71 ± 0·25	0·41 ± 0·08	0·86 ± 0·3	1·13 ± 0·01	0·60 NS	8·93 $P < 0{\cdot}001$
Predator:prey ratio	NA	0·78 ± 0·33	0·89 ± 0·09	0·94 ± 0·16	1·26 ± 0·13	$H = 0{\cdot}4$† NS	$H = 3{\cdot}86$† $P < 0{\cdot}05$

* Experiments were stopped at 130 days.
† Test was a Kruskal–Wallis test on rank predator–prey ratios.

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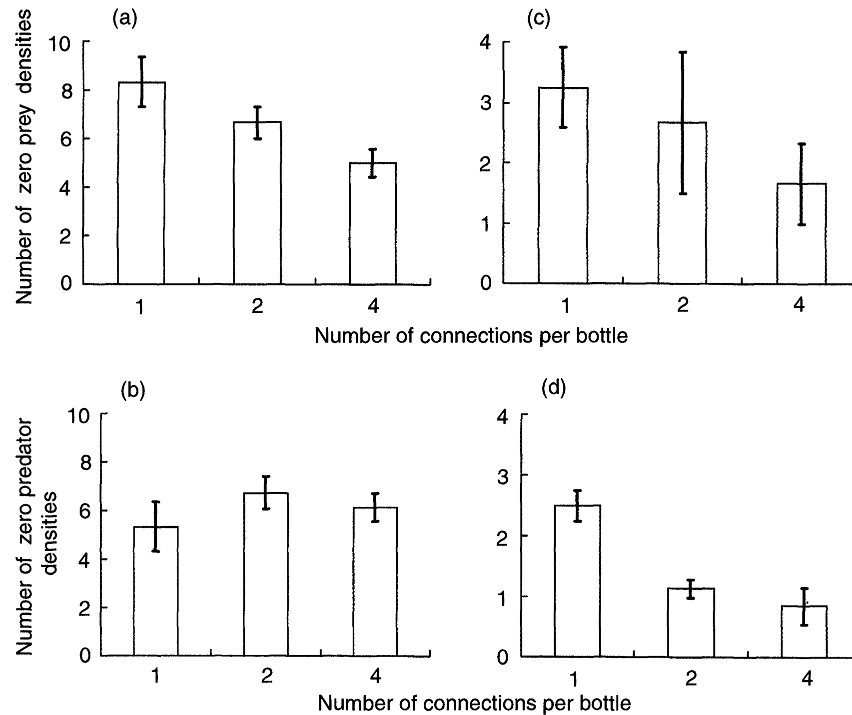

Fig. 4. The frequency of recorded densities of zero in bottles of spatial arrays with different numbers of connecting tubes: (a) and (c) are for prey, *C. striatum*; (b) and (d) are for predators, *D. nasutum*; (a) and (b) are for bottles of 3 × 3 arrays; (c) and (d) are for bottles in 5 × 5 arrays. In each case the number of zero density values is the average of all bottles in all arrays of a given type and comes from a total of 20 observations. Means and standard error bars were calculated using the within-array means from the three replicates of each array type. Note that the panels for *D. nasutum* and *C. striatum* are on different scales. One way ANOVAs were used to compare Ln-transformed numbers of zero densities in bottles with different numbers of tubes. Results were: (a) $F_{2,6} = 5{\cdot}21$, $P < 0{\cdot}05$, (b) $F_{2,6} = 0{\cdot}44$, $P \gg 0{\cdot}05$, (c) $F_{2,6} = 1{\cdot}29$, $P \gg 0{\cdot}05$, (d) $F_{2,6} = 7{\cdot}60$, $P < 0{\cdot}05$.

the maximum possible. However, there were no significant differences in average predator or prey density between nine bottle arrays and the equivalent (270 mL) undivided volume (Table 1).

Predators were more abundant in array bottles that had greater numbers of connections (Fig. 5b, d). This suggests that the level of subdivision at which predators are most abundant is either at, or greater than, the maximum represented in subdivided arrays. We would also expect predator densities to be greater in 25 bottle arrays than in nine bottle arrays, because the former has a greater average number of connections per bottle. This was confirmed by a two-way ANOVA comparing bottles with numbers of connections and different sizes of arrays, followed by sequential Bonferroni tests to identify means that differed ($F_{1,14} = 33{\cdot}8$, $P < 0{\cdot}001$). Conversely, mean densities of prey did not significantly differ between bottles with different numbers of connections (Fig. 5a, c), and array size had no effect on prey densities. There were no significant differences between predator or prey abundances in 270 vs. 750 mL undivided microcosms (in Student's t-tests between mean Ln(density + 1) values), which shows that the differences in predator abundance in nine and 25 bottle arrays were not due to differences in total volume.

In summary, predators were most abundant either at, or above, the rates of dispersal possible in subdivided arrays, but at a lower rate than the maximum possible in this experiment (seen in undivided microcosms). Prey were most abundant at a dispersal rate which is less than the maximum observed, but with the present data we cannot be more precise.

POPULATION VARIABILITY

We compared array bottles with different numbers of connections to test whether local variability changed with dispersal. Results from 25 bottle arrays confirm that population variability of both species was greatest where least dispersal was possible. Predators and prey in 25 bottle arrays had higher coefficients of variation (CVs) of density in bottles that had fewer connections (Fig. 6b, d); sequential Bonferroni tests showed this difference was due to bottles with only one connecting tube having higher CVs than bottles with two or four connecting tubes. There were no significant differences for predators or prey in nine bottle arrays (Fig. 6a, c; tested using one-way ANOVAs), possibly because estimates of CV are less accurate for smaller sample sizes. We did not compare variability between nine and 25 bottle arrays because this comparison would confound differences due to the distance between bottles with those due to levels of dispersal.

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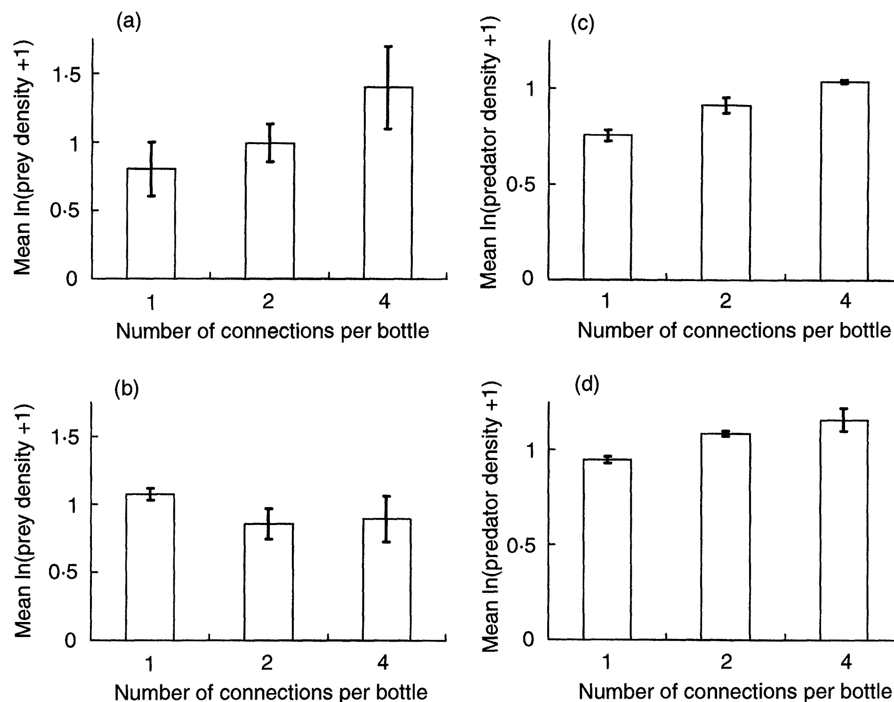

Fig. 5. Average values of Ln(density + 1) in bottles of spatial arrays with different numbers of connecting tubes: (a) and (c) are for prey, *C. striatum*; (b) and (d) are for predators, *D. nasutum*; (a) and (b) are for bottles in 3 × 3 arrays; (c) and (d) are for bottles in 5 × 5 arrays. In each case the mean and standard error were calculated from three averages, one for each array, which avoids pseudoreplication. Note that the panels for *D. nasutum* and *C. striatum* are on different scales. One way ANOVAs were used to compare Ln(mean density + 1) in bottles with different numbers of connecting tubes. Results were: (a) $F_{2,6} = 1{\cdot}90$, $P \gg 0{\cdot}05$, (b) $F_{2,6} = 21{\cdot}3$, $P < 0{\cdot}001$, (c) $F_{2,6} = 0{\cdot}86$, $P \gg 0{\cdot}05$, (d) $F_{2,6} = 9{\cdot}60$, $P < 0{\cdot}025$.

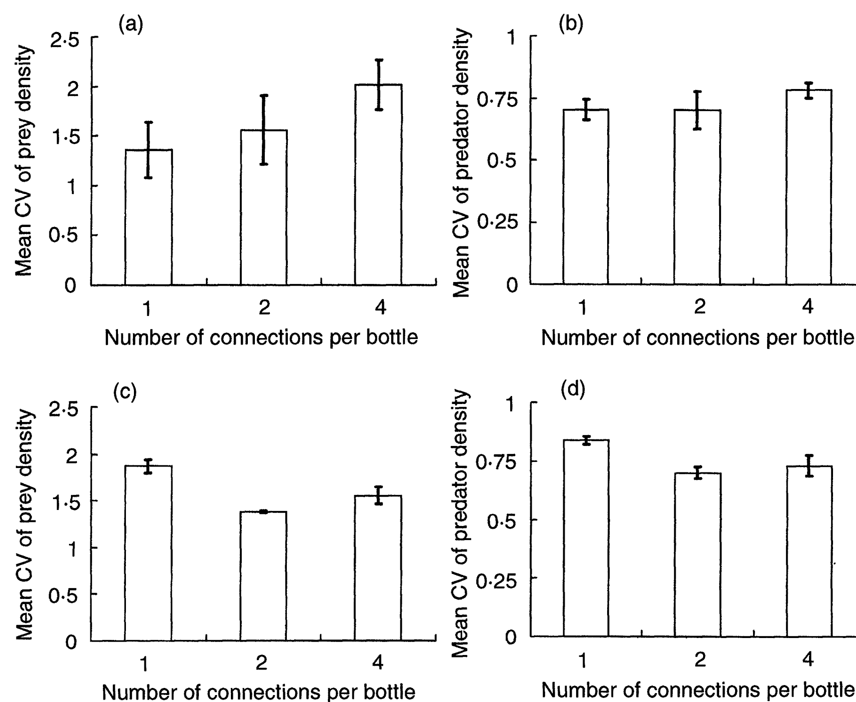

Fig. 6. Average values of the coefficient of variation (CV) of density within bottles of spatial arrays with different numbers of connecting tubes: (a) and (c) are for prey; and (b) and (d) are for predators; (a) and (b) are for bottles of 3 × 3 arrays; (c) and (d) are for bottles in 5 × 5 arrays. CVs were calculated separately for each bottle then these values were averaged for each array. The mean and standard error was then taken of these per array averages to avoid pseudoreplication. Note that the panels for *D. nasutum* and *C. striatum* are on different scales. One way ANOVAs were used to compare natural logarithms of CVs in bottles with different numbers of connecting tubes. Results were: (a) $F_{2,6} = 1{\cdot}27$, $P \gg 0{\cdot}05$, (b) $F_{2,6} = 0{\cdot}83$, $P \gg 0{\cdot}05$, (c) $F_{2,6} = 15{\cdot}3$, $P < 0{\cdot}005$, (d) $F_{2,6} = 5{\cdot}30$, $P < 0{\cdot}05$.

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PREDATOR:PREY RATIOS

There was contradictory evidence that predator:prey ratios were higher where more dispersal was possible. For example, predator:prey ratios were significantly higher in 25 bottle arrays than in undivided 750 mL microcosms, where there were no barriers to dispersal (Table 1). A possible cause for this is that predators may have limited their own density by over-exploiting prey in undivided microcosms. Average prey density in undivided 750 mL microcosms was half of that in 750 mL arrays, possibly indicating over-exploitation in the former. There was no difference between predator:prey ratios in subdivided and undivided 270 mL microcosms (Table 1). In contrast, comparisons of array bottles with different numbers of connections do show the expected pattern of higher ratios where more dispersal is possible, at least within the 25 bottle arrays (Fig. 7). There were no significant differences in predator:prey ratios among types of bottles in nine bottle arrays. We might also expect ratios to be higher in 25 bottle arrays than in nine bottle arrays because the former has more connections per bottle, but only a weak trend was found (Fig. 7; data were analysed via a two-way non-parametric ANOVA, the Scheire-Ray-Hare extension of the Kruskal–Wallis test, on array size and mean number of connections for array sizes $H_1 = 2{\cdot}9$, $P > 0{\cdot}05$). Predator:prey ratios did not vary between undivided 270 and 750 mL microcosms (in a Kruskal–Wallis test), so that the comparison of ratios between subdivided nine and 25 bottle arrays is unlikely to be confounded by volume effects. Hence, we do not have consistent evidence for predator:prey ratios increasing or decreasing with dispersal.

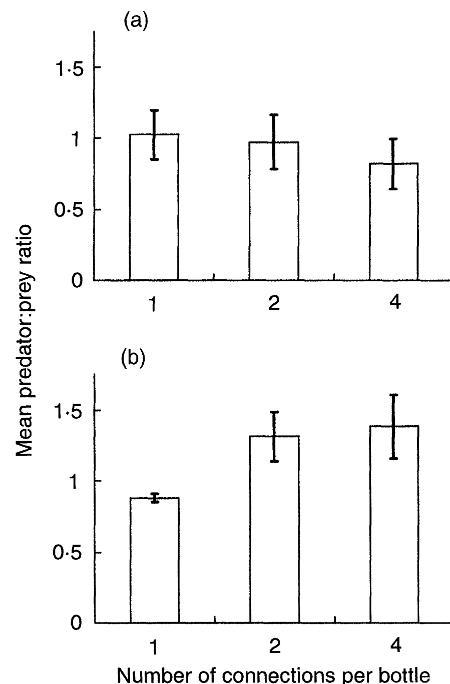

Fig. 7. Mean predator:prey ratios in bottles of spatial arrays with different numbers of connecting tubes: (a) is for nine bottle arrays and (b) is for 25 bottle arrays. Means and standard errors for each type of bottle were calculated from three replicates of per array averages, which avoids pseudoreplication. Kruskal–Wallis tests were used to compare ranks of predator:prey ratios in bottles with different numbers of connections. Results were: (a) $H_2 = 1{\cdot}1$, $P \gg 0{\cdot}05$, (b) $H_2 = 6{\cdot}01$, $P < 0{\cdot}05$, where H has a χ^2 distribution.

ASYNCHRONY AND SPATIAL VARIABILITY

Overall, spatial synchrony did not differ in microcosms that permitted different levels of dispersal. When sample sizes were held constant (Table 2), there were no differences in levels of spatial synchrony in nine or 25 bottle arrays for predators or prey, or in how synchrony changed with distance. Average levels of synchrony were similar in nine and 25 bottle arrays (Student's $t_4 = 0{\cdot}03$, $P \gg 0{\cdot}05$ for prey, and $t_4 = 0{\cdot}15$ for predators, $P \gg 0{\cdot}05$; from calculations of synchrony with similar sample sizes). For predators, the rate at which synchrony declined with distance was identical between nine bottle arrays and nine bottle blocks within 25 bottle arrays (slope, $d = -0{\cdot}16$). For prey, the rate of decline in synchrony with distance was too variable within arrays to perform a similar analysis (e.g. compare 25 bottle arrays with a subsample of nine bottles in Table 2).

Spatial variability was predicted to be lower in bottles which were linked by more dispersal. Within 25 bottle arrays, as predicted, the CV of density for both predators and prey was greater in pairs of adjacent bottles where one bottle had only one connecting tube than in pairs where the second bottle had four connections ($P < 0{\cdot}025$ in t-tests; Fig. 8c, d). No such differences were found in nine bottle arrays (Fig. 8a, b), possibly because of the lower sample size. We might also expect spatial variability to be greater in nine bottle arrays than in 25 bottle arrays, because of the smaller average number of connections per bottle in the former. However, there was no significant effect of microcosm type in a three-way ANOVA comparing spatial variability between species, array sizes and levels of connectivity ($F_{1,20} = 0{\cdot}3$, $P \gg 0{\cdot}05$).

In summary, we did not find a difference in spatial synchrony between microcosms with different levels of connectivity. This presumably reflects the high level of variability in our measures of synchrony (Table 2). However, a more sensitive measure of asynchrony, spatial variability, increased with connectivity of bottles within subdivided microcosms for 25 bottle arrays.

Discussion

In general the predicted effects of dispersal on predator–prey metapopulation dynamics were found in *C. striatum* and *D. nasutum* (Table 3). Predicted effects were found more frequently in comparisons using 750 mL subdivided and undivided microcosms than in 270 mL microcosms (Table 3). This is expected

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Table 2. Spatial synchrony of fluctuations in population density for predators and prey in arrays. Synchrony was quantified using lag zero cross-correlation, *r*, measured using 20 samples taken at 2-day intervals (from day 54). If X_i and X_j are the natural logarithms of density +1 in bottles *i* and *j* of an array at a given time then *r* is the correlation between X_i and X_j (Hanski & Woiwod 1993). We removed a bias caused by simultaneously recorded zero density values in pairs of bottles, as zero density values often reflect simultaneous extinctions rather than similar densities. The table gives multiple regressions of synchrony (*r*) against distance between bottles (slope *d*) and numbers of densities that were zero (slope *z*) in a pair of bottles simultaneously. Distance is in units of the distance between pairs of adjacent bottles. The intercept *a*, gives synchrony at a distance of zero, or the average *r*-value if no slopes were significant. To distinguish sample size effects from real differences between arrays of different sizes, we repeated the regressions in 25 bottle arrays using only a 3 × 3 group of bottles in one corner of the larger 5 × 5 array. Missing values were not significant at $P < 0{\cdot}05$. Regressions were weighted for numbers of non-zero abundance values, and *r*-values from less than 5 pairs of non-zero density values were excluded. Values preceded by a ± symbol are standard errors, and *n* is the total number of *r*-values that were used in the multiple regression. Non-significant slopes (*d* or *z*) were excluded from calculations of mean slopes

		Prey, *C. striatum*			Predators, *D. nasutum*		
Replicate	*n*	*a*	*d*	*z*	*a*	*d*	*z*
Entire nine bottle array							
1	36	0·41 ± 0·07			0·28 ± 0·12	–0·16 ± 0·07	
2	36	0·58 ± 0·02			0·24 ± 0·04		0·10 ± 0·04
3	36	0·53 ± 0·03			0·44 ± 0·03		
Mean		0·51 ± 0·17	NA	NA	0·32 ± 0·19	–0·16	NA
Entire 25 bottle array							
1	300	0·37 ± 0·03			0·22 ± 0·02	–0·03 ± 0·01	0·14 ± 0·04
2	300	0·37 ± 0·04	–0·04 ± 0·01	0·04 ± 0·01	0·47 ± 0·02	–0·05 ± 0·01	0·06 ± 0·02
3	300	0·23 ± 0·04	–0·03 ± 0·02	0·05 ± 0·01	0·28 ± 0·02	–0·06 ± 0·01	
Mean		0·32 ± 0·17	–0·04 ± 0·01	NA	0·32 ± 0·21	–0·05 ± 0·07	NA
9 bottle block from 25 bottle array							
1	36	0·27 ± 0·08	–0·16 ± 0·05	0·07 ± 0·01	0·10 ± 0·04		
2	36	0·83 ± 0·11	–0·18 ± 0·07		0·49 ± 0·03		
3	36	0·46 ± 0·06			0·53 ± 0·10	–0·16 ± 0·07	
Mean		0·52 ± 0·31	–0·17 ± 0·02	NA	0·37 ± 0·28	–0·16	NA

because dynamics could be measured with greater accuracy in 25 bottle arrays than in nine bottle arrays. We also found more significant relationships between dispersal and density in predators than prey (Table 3), possibly because predators had lower population variability than prey (Fig. 6).

We unequivocally confirmed that predator and prey persistence and predator density were highest at intermediate dispersal rates of both predators and prey (Zeigler 1977; Crowley 1981; Nachman 1987b; Reeve 1988; Hassell *et al.* 1991; Comins *et al.* 1992). Prey densities were expected to be higher at lower dispersal rates (Zeigler 1977; Nachman 1987b; Reeve 1988) and we found this pattern when comparing undivided volumes (maximum dispersal) to subdivided volumes (lower dispersal). Local population variability of predators and prey was greater at low dispersal rates of both (in bottles with only one connection), as expected (Reeve 1988). Predator:prey ratios were expected to be greatest at higher dispersal rates (Nachman 1987b); however, evidence for this was equivocal (Table 3), which we discuss in more detail below. Our measures of spatial synchrony were very noisy and we were unable to confirm that spatial asynchrony is greater at lower dispersal rates (Zeigler 1977; Crowley 1981; Nachman 1991). However, we did find an expected consequence of differences in spatial synchrony; spatial population variability was greater at low dispersal rates in array bottles with fewer connections in 25 bottle arrays (Table 3).

Evidence for greater predator:prey ratios at the highest dispersal rates was inconclusive. The comparison of ratios with the greatest power (bottles within subdivided microcosms) showed the expected result (Nachman 1987b). Conversely, comparisons between subdivided and undivided 750 mL microcosms showed that the ratio was highest at dispersal rates which are less than the maximum possible. A possible cause for this difference is that predators within subdivided microcosms appeared to disperse in response to low prey densities. Salt (1979) showed that the swimming rate of predators peaked at 1–5 h of starvation (when at densities equivalent to those in our experiments). We did not know of Salt's relevant work when conducting our experiments, but this mechanism is consistent with our results. Dispersal of starving predators could reduce predator starvation rates, assuming that some predators reach patches with more prey, and prevent predators from overexploiting prey to the same extent as in undivided 750 mL microcosms. Within subdivided microcosms, lower starvation rates would increase average predator densities thereby making average predator:prey ratios greater. Predators that disperse away from low

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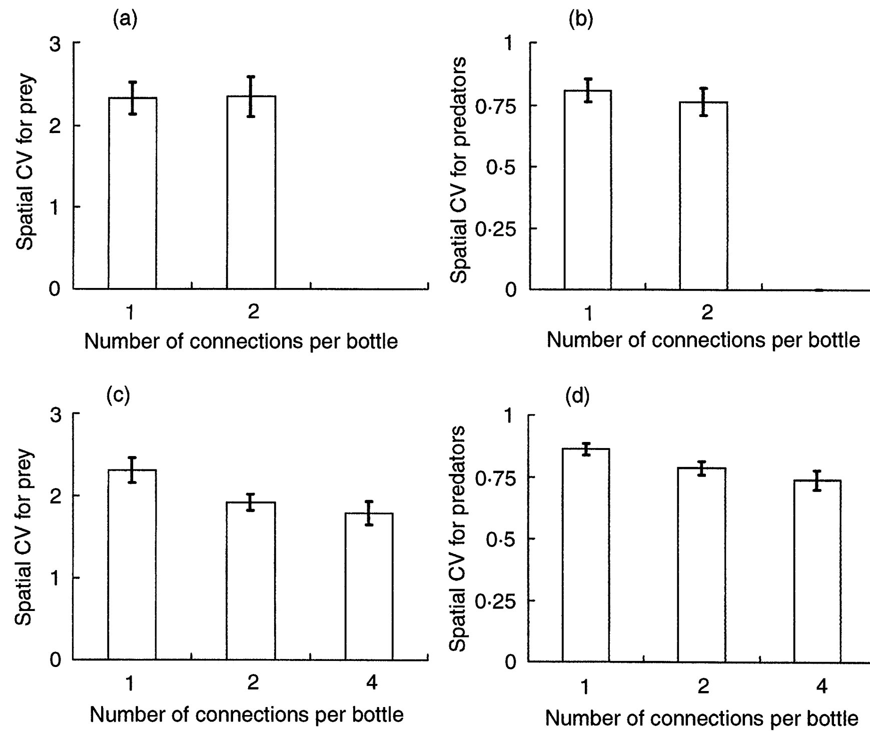

Fig. 8. Spatial population variability of predators and prey in bottles within subdivided microcosms that were linked by different numbers of tubes: (a) and (c) are for prey; (b) and (d) are for predators; (a) and (b) are for bottles of 3 × 3 arrays; (c) and (d) are for bottles in 5 × 5 arrays. Coefficient of variation (CV) were calculated separately for each adjacent pair of bottles, where the first bottle always had four connecting tubes and the second bottle had the number of tubes shown on the *x*-axis. These CV values were averaged for each array and the mean and standard error was then taken of these per array averages to avoid pseudoreplication. Note that the panels for *D. nasutum* and *C. striatum* are on different scales. One way ANOVAs were used to compare natural logarithms of CVs in bottles with different numbers of connecting tubes. Results were: (a) $F_{1,4} = 0{\cdot}01$, $P \gg 0{\cdot}05$, (b) $F_{1,4} = 0{\cdot}40$, $P \gg 0{\cdot}05$, (c) $F_{2,6} = 4{\cdot}11$, $0{\cdot}05 < P < 0{\cdot}1$; however, bottles with one and four tubes differed (Student's $t_7 = 2{\cdot}7$, $P < 0{\cdot}025$), (d) $F_{2,6} = 3{\cdot}79$, $P > 0{\cdot}1$, but bottles with one and four tubes differed ($t_7 = 2{\cdot}7$, $P < 0{\cdot}025$).

Table 3. Summary of predicted and observed effects of dispersal rates of predators and prey on predator–prey metapopulation dynamics. The table lists the dispersal rates of both predators and prey at which the factor will be *greatest*. Lack of significance at $P < 0{\cdot}05$ is indicated by NS and non-applicable results are indicated by NA. In columns for observed dispersal rates, 'low' indicates that the factor was greatest at highest levels of subdivision, 'intermediate' indicates that the factor was greatest at lower levels of subdivision, and 'high' indicates that the factor was greatest in undivided microcosms. We also use < high to indicate that the factor was greatest at either low or intermediate levels of dispersal and we cannot be more precise

Factor	Predicted dispersal rate where factor is greatest	Kind of comparison: Subdivided vs. undivided microcosms 270 mL	Subdivided vs. undivided microcosms 750 mL	Bottles with different connectivity within arrays 270 mL	Bottles with different connectivity within arrays 750 mL	9 bottle vs. 25 bottle arrays
Prey persistence	Intermediate	NS	< High	Intermediate	NS	Intermediate
Predator persistence	Intermediate	< High	< High	NS	Intermediate	Intermediate
Mean prey density	Low	NS	< High	NS	NS	NS
Mean predator density	Intermediate	NS	< High	Intermediate	Intermediate	Intermediate
Local population variability	Low	NA	NA	NS	Low	NA
Predator:prey ratio	High	NS	< High	NS	High or Intermediate	NS
Spatial asynchrony	Low	NA	NA	NS	NS	NS
Spatial population variability	Low	NA	NA	NS	Low	NS

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prey densities would not drive prey down to such low levels of abundance. Therefore, predators may overexploit prey less in subdivided microcosms than in undivided microcosms. Predators are likely to have dispersed via the same mechanism (responding to prey density) in nine and 25 bottle arrays, possibly explaining why ratios did not differ between these. Models of predator–prey metapopulation dynamics generally do not include such realism as the dispersal mechanism changing with the amount of subdivision, or starvation.

The predicted effects of dispersal on predator–prey metapopulation dynamics appear to be very general, varying little with the specifics of the model used (Hastings 1990; Kareiva 1990; Reeve 1990; Taylor 1990, 1991; Hastings & Harrison 1994; Harrison & Taylor 1995). Our data were mainly consistent with the catholic predictions of these models. In only one case (predator:prey ratios) was the outcome inconsistent with observations of dynamics in *C. striatum* and *D. nasutum,* and in this case the prediction came from only one model.

It would be interesting to incorporate predator dispersal in response to prey into a predator–prey metapopulation model to check whether this produces greater predator:prey ratios than density-independent predator dispersal. A model specifically tailored for this system could also tell us at which ratios we expect the various population dynamic factors to be greatest, permitting quantitative comparisons to be made.

Protozoan predator–prey pairs have been shown to be well described by Lotka–Volterra dynamics (Maly 1978; Harrison 1995) and it is perhaps therefore to be expected that they can be well described by very general metapopulation models. We advocate the testing of metapopulation theory using species that are known to depart from the assumptions of simple models and development of appropriate metapopulation models for such systems.

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