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EMPIRICAL EVIDENCE FOR PREDATOR–PREY SOURCE–SINK DYNAMICS

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Abstract. Theory suggests that a source–sink structure for a prey species can promote the persistence of an otherwise nonpersisting predator–prey interaction. Using a heliozoan protist predator, *Actinosphaerium nucleofilum,* and a ciliated protozoan prey species, *Tetrahymena pyriformis,* we tested this prediction in laboratory microcosms. We created subdivided microcosms, each consisting of a 30-mL bottle containing predators and prey connected to a 30-mL bottle containing prey only. Prey dispersed freely through this connection, but predators did not disperse for hundreds of prey generations. The predators and prey in the subdivided microcosms persisted for over three times as long as they did in undivided 30-mL and 60-mL bottles. Our results suggest that prey rescue effects and spatial asynchrony in prey dynamics, characteristic metapopulation features, enhanced persistence in the subdivided microcosms. However, the details by which persistence was achieved closely resemble source–sink dynamics, not classic metapopulation dynamics. Evidence suggests that continuous prey immigration into predator–prey bottles from extinction-invulnerable prey-only bottles may have weakened the coupling between predator and prey dynamics and contributed to the increase in persistence. In showing that source–sink dynamics enhanced predator–prey persistence, our experiments support conclusions of metapopulation theory that point to the importance of immigration between spatially discrete populations.

Key words: Actinosphaerium nucleofilum; *metapopulation; microcosm; persistence; predator–prey; refuge; source–sink; protozoa; spatial population dynamics;* Tetrahymena pyriformis.

INTRODUCTION

Most organisms reside in patchy environments comprising either collections of habitat patches of varying quality or a single habitat containing patchily distributed resources. For studying spatial population dynamics in the former, ecologists have formulated a framework: "source–sink dynamics" (Pulliam 1988, 1996, Pulliam and Danielson 1991, Holt 1985, 1993, Hanski and Simberloff 1997). In a source–sink system, individuals inhabit both high-quality source and low-quality sink patches. As defined by Holt (1985, 1993) and Pulliam (1988), a source patch is one in which reproduction exceeds mortality at equilibrium and a sink patch is one in which the reverse is true. Net migration of individuals from a source to a sink patch allows the source and sink populations to equilibrate.

Immigration of individuals to a sink patch from source patches forestalls extinction in the sink patch; at a low sink density it promotes a positive rate of increase. This "rescue effect" (Brown and Kodric-Brown 1977) is also responsible for preventing subpopulations from going extinct in many metapopulation models. Isolating a source patch from immigration does not adversely impact its viability since its persistence depends entirely on local dynamics. However, isolating a sink patch may either cause a decline to extinction or equilibration at a smaller population size. In the case of persistence despite isolation, a loss of immigration leads to a reduction in abundance which leads to a density-dependent increase in birth rate or a density-dependent decrease in death rate. Watkinson and Sutherland (1995) call sink populations of this type "pseudo-sinks."

Ecologists have extended the domain of source–sink theory to interacting species. Danielson (1992), Holt (1993), and Loreau and De Angelis (1997) have investigated the impact of a source–sink structure on competing species and Holt (1985, 1993) has studied source–sink dynamics in a predator–prey context. In each of two different models, Holt (1985, 1993) considers two patches which form a source–sink structure. The predator–prey interaction is confined to one patch (a predator–prey patch) and the other patch contains prey only. The dynamics are mathematically unstable in the predator–prey patch when it is isolated from the other patch. He demonstrates that for many parameter combinations a source–sink structure for the predators or prey tends to stabilize the predator–prey interaction in the predator–prey patch. It appears that mathematical stability is achieved by a prey rescue effect.

Source–sink dynamics shares a number of characteristics with classic metapopulation dynamics (see Crowley 1981, Taylor 1990, 1991, Holyoak and Lawler 1996, Hanski and Gilpin 1997). In a persisting classic metapopulation, all populations are susceptible to ex-

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tinction, but spatially asynchronous dynamics prevents global extinction. The mechanism that promotes persistence of local populations in both types of dynamics is immigration combined with spatial asynchrony in dynamics. This ensures that there is always a source of individuals to prevent a population from going extinct (through the rescue effect) or to re-establish a population that has gone extinct (e.g., Levins 1970). The difference between the two types of systems is in the way each one generates asynchrony. In a stable source–sink system, dynamics are asynchronous because the source population is not susceptible to extinction; it cannot attain a very low density at the same time a sink population does. As a consequence, the regional persistence of a source–sink systems depends entirely on the persistence of the stable source populations: without them, the entire system goes extinct. This is not true for a classic metapopulation (i.e., Levins 1970) which can persist despite the lack of a stable population.

Parallels also exist between predators and prey persisting through source–sink dynamics and through refuges for prey from predators. Defined broadly, refuges reduce predation pressure on prey (Sih 1987). In this sense, a source patch which is void of predators may been seen as a type of refuge for prey. However, research on refuges for prey from predators has typically focused on a well-mixed prey population of which some members experience a smaller risk of predation than others (reviewed by Murdoch and Oaten 1975, Hassell 1978, Taylor 1984, Sih 1987, Murdoch et al. 1996). This suggests that movement between patches is common. Movement in and out of refuges is implicit (space is not explicitly modeled). Source–sink models, on the other hand, typically assume that source individuals belong to a different population than the sink individuals. This implies that movement between patches is rare. The models explicitly track the movement between patches and the dynamics within patches (e.g., Davis and Howe 1992). Refuge theory emphasizes that mathematical stability is achieved by within-population density dependence: an increase in the proportion of prey residing in the refuge as prey density decreases or predation pressure increases (Sih 1987). However, a source–sink structure confers mathematical stability through between-population density dependence mediated by rescue effects.

Despite the logic of the theory and the abundance of patchy predator–prey systems, a recent review has found no unequivocal examples of predator–prey systems that persist via source–sink dynamics, largely because detailed records of population dynamics are difficult to obtain (Pulliam 1996). To assess the relevance of source–sink theory to experimental predator–prey systems, we conducted experiments in laboratory microcosms. We used microcosms to test source–sink theory because they are amenable to a high degree of control of variables such as patch configuration, patch quality, and species composition. Microcosms also help to refine theory by identifying biological features that have been ignored by theoreticians (reviews: Drake et al. 1996, Lawler 1998). Microorganisms, in particular, are very tractable subjects for spatial population studies. The short generation times facilitate the collection of data representing thousands of generations in a relatively short time span. Furthermore, replication of entire spatially distributed populations of small organisms is also feasible.

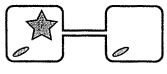
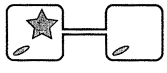
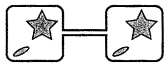
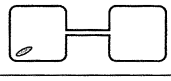
We conducted three experiments to determine if source–sink dynamics could enhance the persistence of predators and prey. The purpose of the first experiment was to determine if spatial subdivision of microcosms was capable of enhancing the persistence of two protist species which do not coexist in undivided microcosms (M. Holyoak, *unpublished data*): the bacterivorous ciliate *Tetrahymena pyriformis* (a prey species) and the heliozoan *Actinosphaerium nucleofilum* (a predator species). In the second experiment, we examined the dynamics operating in spatially subdivided microcosms to determine if classic metapopulation dynamics was sufficient to promote persistence. In the third experiment, we estimated the migration rate of prey and the influence of prey emigration on the local dynamics of the prey-only bottles of the spatial microcosms of the first experiment. An outline of the design and purpose of each experiment is provided by Table 1.

Methods

The protozoa

Bacterivorous *Tetrahymena pyriformis* and *Actinosphaerium nucleofilum* were obtained from Carolina Biological Supply (Burlington, North Carolina, USA). Under our standard culture conditions (see *Methods*: *Experiment 1*), *T. pyriformis* divides by binary fission every 6.3 hr at room temperature (see *Methods*: *Experiment 1* and *Experiment 2*) when supplied with abundant bacterial food (see Holyoak and Lawler 1996 for method of calculation). The doubling time of the heliozoan sarcodine *A. nucleofilum* under the present experimental conditions and with abundant prey was ~13.7 hr (M. Holyoak, *unpublished data*). In the absence of protozoan prey *Actinosphaerium* starves rapidly (M. Holyoak, *unpublished data*). *Actinosphaerium* is a sit-and-wait predator that feeds phagotrophically. *Tetrahymena* that collide with *Actinosphaerium* adhere to the viscid mucous coating *Actinosphaerium*'s radial arms (axopods) and to extrusomes (mucocysts) discharged by the predator (reviewed by Febre-Chevalier 1990). Although *Actinosphaerium* moves up to a few millimeters per hour (M. Holyoak, *unpublished data*), it dispersed between microcosm bottles only once every few hundred prey generations (see *Results*). The species are neither cannibalistic nor do they form resting cysts under the present experimental conditions.

TABLE 1. Experimental design of treatments within each experiment.

Experiment		Purpose
Experiment 1		
1) 	30-mL prey-only (3)	Control, to ensure that prey populations persisted in the absence of predators
2) 	30-mL (6)	To assess predator–prey persistence in undivided 30-mL microcosms
3) 	spatial (6)	To determine if spatial habitat structure had an effect on predator–prey persistence
4) 	60-mL (6)	To determine if population size had an effect on predator–prey persistence.
Experiment 2		
1) 	Single predator (6)	Control, to assess predator–prey persistence when metapopulation dynamics are not feasible
2) 	Double predator (6)	To determine if metapopulation dynamics had an effect on predator–prey persistence
Experiment 3		
	All (20)	To characterize the per capita emigration rate

Notes: An oval indicates the presence of bacterivorous *T. pyriformis*, and a star indicates the presence of predator *A. nucleofilum*. Numbers in parentheses refer to the number of replicates.

Experiment 1: Do spatial dynamics increase persistence?

To determine whether regional processes could enhance the persistence of predators and prey, we established four treatments (Table 1): (1) isolated 30-mL bottles containing only prey (three replicates); (2) isolated 30-mL bottles containing predators and prey (six replicates); (3) connected pairs of 30-mL bottles, one bottle of each pair (randomly selected) containing prey and the other bottle containing predators and prey (six replicates); (4) isolated 60-mL bottles containing predators and prey (six replicates). We compared the time series of densities in various pairs of treatments. We compared Treatments 1 and 2 to verify that predators and prey are unable to coexist in undivided microcosms and that this is due to the interaction, not the inability of the prey to survive in culture. Comparison of the dynamics in Treatment 2 with the dynamics in predator–prey bottles of Treatment 3 allows us to assess the ability of spatial dynamics to enhance persistence. Treatment 4 controls for a patch-size effect.

Predators and prey were cultured in microcosms containing sterile nutrient medium inoculated with a mixed-bacteria suspension. Three types of microcosms were used in Experiment 1: an isolated 32-mL bottle containing 30 mL of medium (Treatments 1 and 2), a connected pair of 32-mL polypropylene bottles containing 60 mL of medium (Treatment 3), and an isolated 240-mL glass bottle containing 60 mL of medium (Treatment 4). In Treatment 3 the polypropylene bottles were connected by a tube (2.0–3.2 mm in diameter and 11.2 cm in length) which allowed prey to pass freely between bottles, but nearly completely prevented predator dispersal (see *Results*). The depths of medium in all three kinds of microcosms were similar. Microcosms were kept at room temperature (23.0°C, SD = 0.81°C). The ambient lighting was not controlled because our systems were free from photosynthetic organisms. In general, the room was lit during daylight hours. Sterile nutrient medium was prepared by adding one crushed Protozoan Pellet (Carolina Biological Supply) to 1 L of a sterile 50:50 mixture of distilled and spring water. Microcosms were inoculated by adding 1 drop (0.03 mL) of a bacterial solution to each 10 mL of sterile medium and one millet seed per 30 mL of medium to provide a slow release of nutrients. We did not track pH or nutrient levels, but the results provided no evidence for systematic variation in population dynamics that might have been caused by fluctuations in these.

After establishing the microcosms, we added prey and predators and began sampling densities. One day after inoculating the microcosms with bacteria, we removed 0.14 mL of solution from each 30 mL and replaced the volume withdrawn with an equivalent vol-

ume of *T. pyriformis* culture containing ~1215 cells/mL. Ten days later we added four predators to the predator–prey bottles of Treatments 2, 3, and 4. Two days after that we began sampling. Every other day, 10% of the volume of each microcosm bottle was carefully withdrawn to avoid inducing flow between bottles. A subsample of five drops (exact sample volumes were determined by weight) was then examined with a binocular microscope to count the number of *T. pyriformis* cells. The entire sample was examined to obtain a census of *A. nucleofilum.* The volumes removed were replaced with sterile nutrient medium. For each microcosm, sampling continued until predators or prey went extinct or until 104 days had elapsed, whichever came first. We adapted a procedure from Holyoak and Lawler (1996) that allowed us to reliably record extinctions.

To assess the effect of treatment on predator–prey dynamics, we calculated the persistence time of the predator–prey interaction, the minimum prey density during the first predator–prey cycle, the long-term prey density, and the strength of the coupling between predator and prey temporal dynamics. Persistence of a replicate was measured as the number of days during which both predators and prey remained extant and, in spatial microcosms, no predator dispersal occurred, up to 104 days (the duration of the experiment). This measure of persistence differs from that typically used. In some cases it underestimates the actual persistence as the predator–prey interaction would have persisted for greater than 104 days had the experiment not been terminated. We tested for significant differences between treatment means by using a nonparameteric procedure that is appropriate for right-censored survival data with multiple treatments. We calculated a chi-square approximation of Peto and Peto's generalized Wilcoxon test (Peto and Peto 1972, Fox 1993). To identify specific treatment means that differed, we performed this test on pairs of treatment means. We compared the minimum prey densities during the first predator–prey cycle to ensure that time interval examined was constant across treatments. We defined the end of the first cycle as the day predators went extinct in the nonspatial 30-mL replicate that was the first to suffer a predator extinction. A one-way ANOVA was used to compare the minimum ln (prey density + 1) between the treatments. We compared the long-term prey density (the mean between days 44 and 64) of the prey-only bottles of the spatial microcosms to the long-term prey density of the nonspatial 30-mL prey-only bottles. We used a one-tailed Student's t test on ln (prey density + 1)-transformed data, hypothesizing that emigration would reduce prey density. Two replicates were excluded from analysis: One replicate of the nonspatial 30-mL bottles was accidentally destroyed and the prey-only bottle of one replicate of the spatial microcosms experienced a predator colonization.

Modeling work predicts that strongly interacting consumer–resource pairs can cause large oscillations, which in turn can cause population densities to become periodically very small and increase the chance of stochastic extinction (McCann et al. 1998). We examined the effect of treatment on predator–prey interaction strength to determine if differences in interaction strength were associated with differences in persistence. We regressed persistence in each predator–prey bottle against a measure of interaction strength then we compared the mean interaction strength between treatments with Student's t tests. We assessed the strength of the predator–prey interaction by modifying a procedure by Pfister (1995). Pfister (1995) quantified interaction strength between competing species by basing a regression model on solutions to the Lotka-Volterra competition equations. Using the two species' time series of densities, she regressed an expression containing one species' density against an expression containing both species' densities and used the resulting correlation coefficient as a measure of the competition coefficient. Pfister showed that this technique was fairly successful at predicting the results of experimental manipulations. However, this procedure is only valid for time-series observations that are independent. As time-series observations are typically autocorrelated, we used a time-series statistic, specifically the cross-correlation coefficient between the time series of densities, as our measure of interaction strength. As in Pfister (1995), our technique has some advantages over performing an additional experiment to assess interaction strength. It quantifies interaction strength using data across a range of densities and does not require additional experiments in which conditions could differ from the original experiment.

For each predator–prey bottle, we calculated a cross-correlation coefficient. We first transformed the predator and prey series of densities to series of ln (density + 1) and truncated each series after the end of the first predator–prey cycle (nine observations) to ensure the interval of time encompassed by each series was constant across treatments. Then we removed linear trends from each transformed series because cross-correlation analyses are very sensitive to nonstationarity (Chatfield 1996). The cross-correlation coefficient, $r_{pv(k)}$, between the predator time series, $\{p_t\}$, and prey time series, $\{v_t\}$, lagged by k observations is determined as follows (Chatfield 1996):

$$r_{pv(k)} = \begin{cases} \dfrac{1}{N\sqrt{s_p^2 s_v^2}} \displaystyle\sum_{t=1}^{t=N-k} (p_t - \bar{p})(v_{t+k} - \bar{v}) \\ \qquad\qquad k = 0, 1, \ldots, N-1 \\ \dfrac{1}{N\sqrt{s_p^2 s_v^2}} \displaystyle\sum_{t=1-k}^{t=N} (p_t - \bar{p})(v_{t+k} - \bar{v}) \\ \qquad\qquad k = -1, -2, \ldots, -(N-1) \end{cases}$$

where N is the number of observations in the time series, s^2 is the sample variance, and a bar signifies the

arithmetic average of the series. Lags up to ±3 were examined, but we report only the lag-zero result, which was representative of other lags. The statistical properties of the measure of interaction strength are poorly known; the results of this analysis should be regarded as suggestive, warranting further investigation.

To determine whether traditional mechanisms of refuge-induced stability were operating in the spatial microcosms, for each spatial-microcosm replicate we regressed the proportion of prey in the prey-only bottle against the microcosm-wide prey density. Each sampling date corresponded to one observation. Significance of the resulting Pearson's correlation coefficient was assessed using a randomization technique as the time-series observations were not independently distributed. The significance level (P) in a one-tailed test was the proportion of ten thousand randomly generated correlation coefficients more negative than the actual one (Manly 1991). Each randomly generated correlation coefficient was obtained by randomly pairing each observed prey density in a time series with an observed proportion from the same series.

Experiment 2: Source–sink or metapopulation structure?

The purpose of this experiment was to determine if metapopulation dynamics could enhance the persistence of predator–prey dynamics in spatial microcosms like those used in Experiment 1. We established two treatments, each replicate comprising a pair of connected 30-mL bottles (Table 1): (1) a predator–prey bottle connected to a prey-only bottle (single-predator spatial microcosm)—six replicates; (2) a pair of connected predator–prey bottles (double-predator microcosms)—six replicates. Experimental procedures and analysis were identical to Experiment 1, with the following exceptions. The medium was inoculated by adding 5 mL of filtered bacteria to 1 L of sterile medium. After 28 hours, *T. pyriformis* were added to yield a density of 291 cells/mL and this prey culture was dispensed into each 30-mL bottle. Five days later 5 mL was removed from each bottle and replaced with fresh sterile medium. Four predators were then added to a randomly selected bottle of each of the single-predator microcosms and two predators were added to each bottle of the double-predator microcosms. Two days later we initiated the sampling regime used in the first experiment. The experiment ran for 50 days with persistence of a replicate curtailed whenever a predator extinction occurred (in either or both bottles). The microcosms were kept at room temperature (22.6°C, SD = 0.64°C). In addition to the measures taken in Experiment 1, we also calculated the lag-zero cross-correlation coefficient to characterize the spatial synchrony between the density fluctuations of the two prey populations in each of the replicates. Due to the existence of serial autocorrelation we used the randomization procedure described for Experiment 1 to determine significance. For each replicate, the proportion of randomly generated correlation values larger in magnitude than the observed value was the two-tailed significance level (P).

Experiment 3: Dispersal rates

The purpose of this experiment was to estimate the amount of emigration from connected prey-only bottles. This is useful for distinguishing between source–sink and refuge dynamics and evaluating why the long-term prey density in the nonspatial 30-mL prey-only bottles was greater than that in the prey-only bottles of the spatial microcosms of Experiment 1. Some possible explanations include: (1) a direct reduction in prey density due to emigration, (2) an indirect reduction due to a loss of nutrients accompanying prey emigration, or (3) a release by predators of a prey toxin. We established 20 microcosms, each comprising a connected pair of 30-mL bottles. A randomly selected bottle of each microcosm served as the origin of emigrants. From each origin bottle a volume of solution was removed and replaced with the same volume of a high-density prey culture solution. In experiments with a closely related ciliate, *Colpidium striatum,* Holyoak (M. Holyoak, *unpublished data*) demonstrated that dispersal rates were greatest under these conditions. We established five replicates of four types of microcosm: removal of 22, 50, 63, or 83 percent of the volume of the origin bottle. After 1–5 hours of dispersal, the bottles were sampled using the same procedure as in Experiment 1 and the exact duration of dispersal was recorded.

We assessed the maximum impact direct emigration would have on the equilibrium density in the nonspatial 30-mL bottles by parameterizing with this dispersal data a simple model, the continuous logistic equation with density-dependent emigration:

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right) - e(N)N.$$

If emigration of individuals was solely responsible for the disparity between the mean long-term prey density in the spatial-microcosm prey-only bottles and the density in the nonspatial 30-mL bottles, then the model equilibrium should be similar to the density in the spatial microcosms. To obtain the emigration function, $e(N)$, the proportion emigrating per generation was regressed against the initial prey density in the origin bottles, with each pair of connected bottles serving as an observation. Data on the doubling time at low density and at room temperature were used to estimate r, the maximum growth rate, and the mean long-term density of prey in the nonspatial 30-mL prey-only bottles of Experiment 1 was used as an estimate of K, the carrying capacity. We used a Student's t test on ln (density + 1)-transformed data to assess the significance of the difference between the model equilibrium and

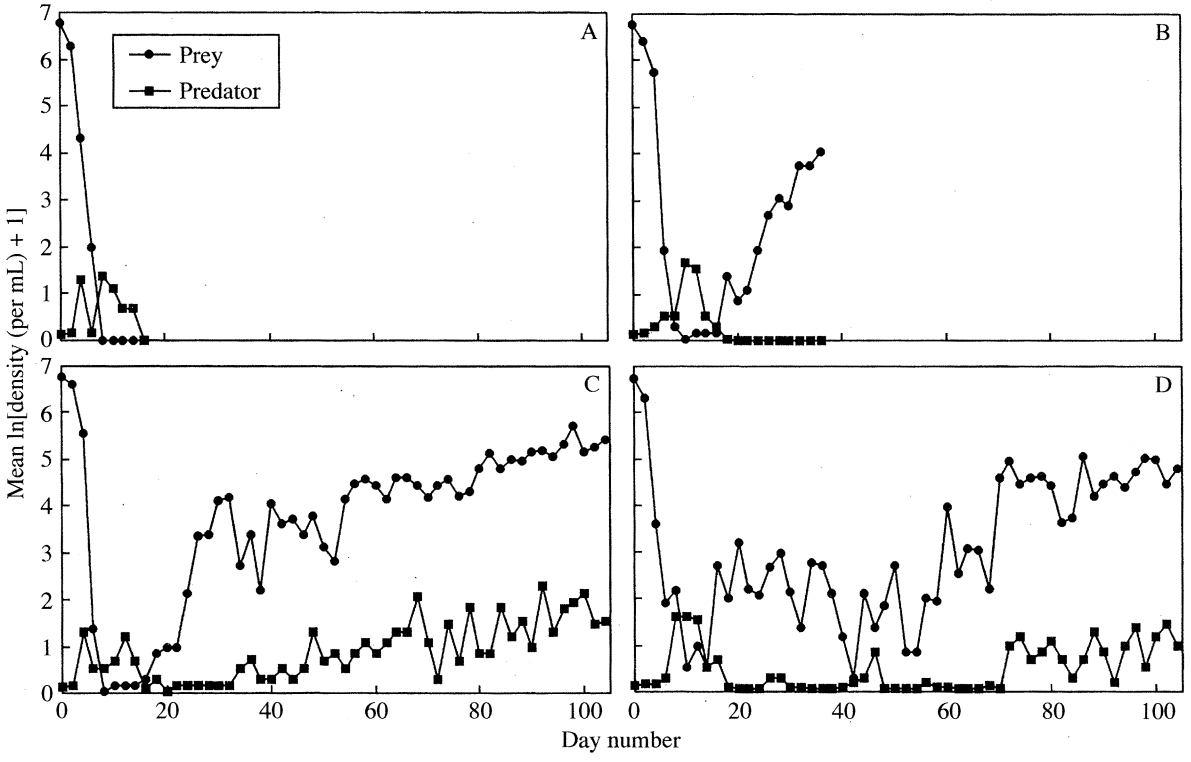


FIG. 1. Time series representative of the populations in Experiment 1. Panels (A), (B), and (C) illustrate the three types of dynamics in isolated, 30-mL predator–prey bottles. In panel (A) both species go extinct; in panel (B) prey remain extant, but predators go extinct; and in panel (C) neither species goes extinct. Panel (D) shows the dynamics typical in predator–prey bottles of the spatial microcosms. (Fig. 4 shows the dynamics typical of the prey-only bottles of this experiment.)

the actual average prey density in the prey-only bottles of the spatial microcosms.

RESULTS

Experiment 1: Do spatial dynamics increase persistence?

Fig. 1 shows representative time series of the population dynamics in Experiment 1. Spatial dynamics extended the persistence of the predator–prey interaction. Predators and prey in the spatial microcosms persisted for ~350 prey generations, over three times as long as predators and prey in nonspatial 30-mL microcosms and predators and prey in nonspatial 60-mL microcosms (Table 2, Fig. 2A). These differences were significant in a chi-square approximation of Peto and Peto's generalized Wilcoxon test (Table 2). This in-

TABLE 2. Summary statistics for 30-mL, 60-mL, and spatial microcosms of Experiment 1.

Means	Microcosm type			Statistic†
	30-mL	60-mL	Spatial	
Type of extinction: predators only, both, neither	3, 2, 1	4, 2, 0	0, 0, 6	
Persistence (d)	30.3[a]	29.0[a]	91.7[b]	$\chi^2_2 = 7.68$, $P = 0.02$
Predator–prey correlation ($\bar{r}_{pv(0)}$)	−0.475[a]	−0.442[a]	0.090[b]	spatial vs. 30-mL, $t_8 = 3.5$, $P < 0.005$; spatial vs. 60-mL, $t_{10} = 3.8$, $P < 0.005$; 30-mL vs. 60-mL, $t_8 = 0.2$, $P \gg 0.05$
Minimum ln(prey density + 1)	0.022[a]	0.016[a]	0.340[b]	$F_{2,15} = 29.6$, $P < 0.00001$
Long-term prey density (no./mL) in prey-only bottles	238.1[a]	...	74.9[b]	one-sided $t_5 = 2.09$, $P < 0.05$
Long-term prey density (no./mL) in predator–prey bottles		...	9.9	...

Notes: Type of extinction refers to the number of microcosms in each treatment that experienced a global predator extinction, a global predator and a global prey extinction, or neither a global predator nor a global prey extinction. Means were taken over all replicates within each treatment, except where noted in text. Means annotated by the same letter did not differ significantly at $P < 0.05$.

† Significance of effect of treatment on dependent variable (except that for $\bar{r}_{pv(0)}$ a comparison of pairs of means is reported).

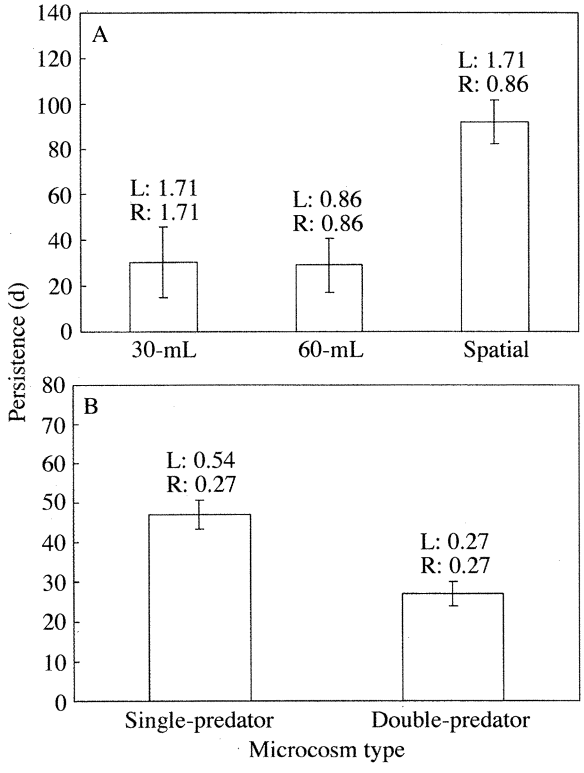


FIG. 2. The mean persistence time of predators and prey for each microcosm type in (A) Experiment 1 and (B) Experiment 2. Persistence of a replicate microcosm is the number of days all populations remained extant prior to the first successful colonization of a prey-only bottle by a predator from a predator–prey bottle, up to 104 days (the duration of the experiment). Within each panel, means annotated with different letters differed at $P < 0.01$; means annotated with the same letter did not differ significantly ($P \gg 0.05$). L and R refer to the local (within the predator–prey bottle of the microcosm) and regional (within the microcosm) initial predator–prey ratios ($\times 10^4$).

creased persistence was not due to the larger size of the spatial microcosms: there was no significant difference between persistence times of the nonspatial 30- and 60-mL microcosms (Table 2, Fig. 2A). The most common route to loss of persistence in the nonspatial bottles was predator extinction when prey densities were low (Table 2). Although predators and prey never went extinct in the spatial microcosms, a predator successfully emigrated from the predator–prey bottle to the prey-only bottle in each of four replicates between days 99 and 104. This resulted in termination of these replicates, but the mean persistence time of these four was ~385 prey generations. In one replicate a predator colonization occurred at 43 days (164 prey generations).

The strength of the coupling between predator and prey dynamics may have influenced persistence. Persistence was correlated with the lag-zero cross-correlation coefficient (Fig. 3A; regression equation: Persistence = $166.6 \times r_{pv(0)} + 98.1$). Furthermore, the predator–prey coupling in the spatial microcosms was weaker than that in either the 30- or 60-mL nonspatial microcosms; the mean correlation in the spatial microcosms was significantly smaller in magnitude than the correlation in the nonspatial 30-mL bottles and than that in the 60-mL bottles (Table 2). The last two did not differ significantly from each other (Table 2).

Three other results provide insight into the dynamics in the spatial microcosms. There was strong evidence for the occurrence of prey rescue effects in the spatial microcosms. A significant effect existed of treatment on the minimum ln (prey density + 1) in predator–prey bottles (Table 2). Minimum ln (prey density + 1) in the spatial microcosms was significantly greater than that in the isolated 30-mL bottles and than that in the isolated 60-mL bottles (Table 2). By contrast, there was little evidence for the existence of stabilizing factors typically associated with a refuge. A significant negative correlation between the proportion of the prey in the spatial microcosms that were located in the prey-only bottles and the microcosm-wide prey density existed for only one replicate out of six ($r = -0.5662$, $P < 0.001$ determined by a randomization test). Of the

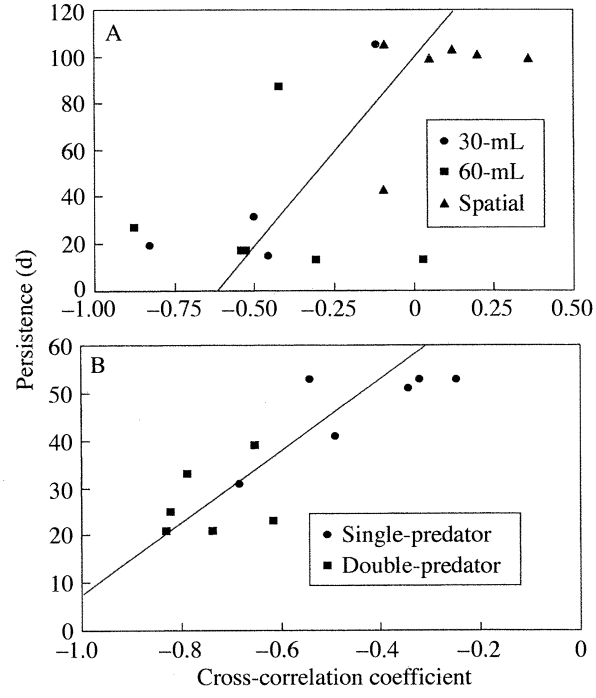


FIG. 3. The relationship between mean persistence time of predators and prey and the lag-zero predator–prey cross-correlation coefficient ($r_{pv(0)}$) for Experiment 1 (panel A; regression equation: Persistence = $166.6 \times r_{pv(0)} + 98.1$; $R^2 = 0.46$) and Experiment 2 (panel B; regression equation: Persistence = $76.0 \times r_{pv(0)} + 81.8$; $R^2 = 0.74$). The lag-zero predator–prey cross-correlation coefficient ($r_{pv(0)}$) for a replicate is the correlation between the ln(density + 1)-transformed predator and prey densities with a lag time of zero days. The regressions were significant at $P < 0.005$ for both experiments.

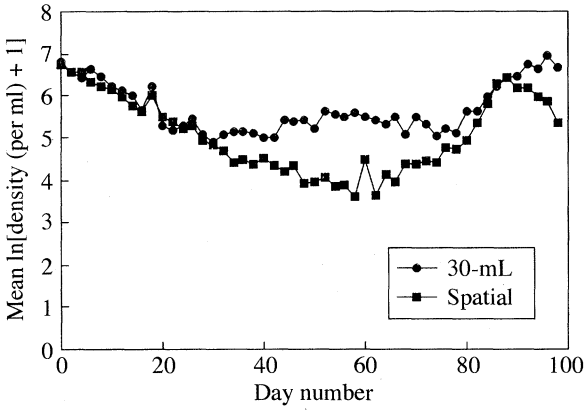


FIG. 4. Time series of mean ln(prey density + 1) in isolated 30-mL bottles and the prey bottles of the spatial microcosms of Experiment 1. The mean prey density during days 44–64 was 238 prey/mL in the 30-mL bottles and 75 prey/mL in the spatial microcosms. The mean of the ln(density + 1)-transformed densities in the 30-mL bottles was significantly larger than that of the spatial microcosms (one-sided $t_5 = 2.09$, $P < 0.05$).

other pairs of bottles, correlations were positive in four cases and negative in one, but no correlation was significant at $P < 0.1$ despite a sample size of 52 in each.

Finally, the mean ln (long-term prey density + 1) in the nonspatial 30-mL prey-only bottles was significantly greater than the mean in the prey-only bottles of the spatial microcosms (Table 2). The prey density declined for ~44 days, at which time the populations began to fluctuate about a mean level of 238 prey/mL in the nonspatial 30-mL prey-only bottles and 75 prey/mL in the connected prey-only bottles (Fig. 4).

Experiment 2: Source–sink or metapopulation structure?

Figure 5 shows time series representative of the population dynamics in Experiment 2. Predators and prey in the single-predator microcosms persisted significantly longer than they did in double-predator microcosms (Table 3, Fig. 2B). In four single-predator microcosms, predators and prey persisted for the duration of the experiment, for 50 days (Table 3). In one microcosm, the predator went extinct after 31 days and in another a predator emigrated from the predator bottle to the prey-only bottle on day 41. Both these events resulted in the termination of the replicate. In four double-predator microcosms, predators went extinct in

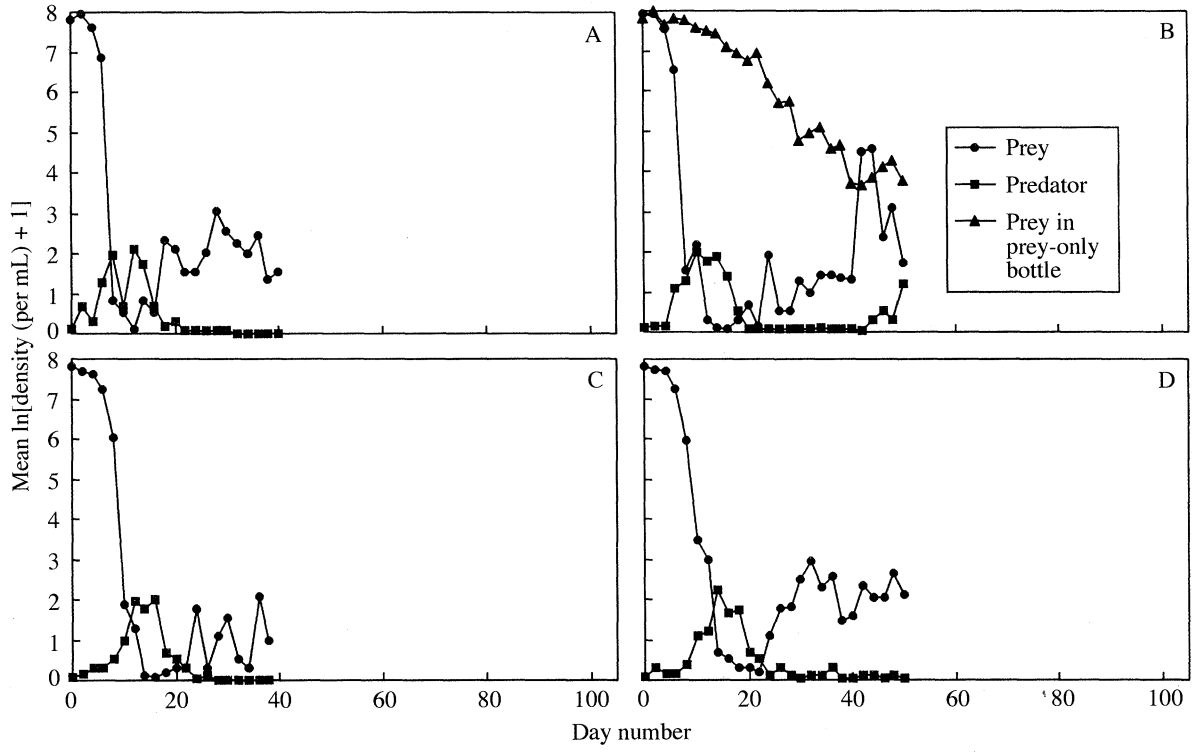


FIG. 5. Time series representative of the populations in Experiment 2. Panels (A) and (B) show the dynamics typical in the single-predator microcosms. In panel (A), predators go extinct and prey remain extant in the predator–prey bottle, and in panel (B), both species remain extant in the predator–prey bottle (and prey remain extant in the prey-only bottle). Panels (C) and (D) are typical of the predator–prey bottles in the double-predator microcosms. In panel (C), predators go extinct and prey remain extant, and in panel (D), both remain extant.

TABLE 3. Summary statistics for the single-predator-population and double-predator-population microcosms of Experiment 2.

Statistic	Microcosm type		Statistic
	Double predator	Single predator	
Type of extinction: predators only, both, neither	4, 0, 2	1, 0, 5	...
Means:			
Persistence (d)	27	47	$X^2_1 = 5.33$, $P = 0.02$
Predator–prey correlation ($\bar{r}_{pv(0)}$)	−0.741†	−0.439	$t_{10} = 3.99$, $P < 0.01$
Minimum ln(prey density + 1)	0.208†	0.140	$t_{10} = -1.03$, $P = 0.33$
Long-term prey density (no./mL) in prey-only bottles	N/A	201.3	...
Long-term prey density (no./mL) in predator–prey bottles	N/A	7.7	...
Prey spatial correlation ($\bar{r}_{v1v2}(0)$)	0.96†	0.52	$t_{10} = 7.60$, $P < 0.001$

Notes: Type of extinction refers to the number of microcosms in each treatment that experienced a global predator extinction, a global predator and a global prey extinction, or neither a global predator nor a global prey extinction. Means were taken over all replicates within each treatment, except where noted in text.

† The value for each replicate was the average of the values in the two bottles.

both bottles. In the other two, predator extinction occurred in only one bottle, resulting in a single predator population in each microcosm at the end of the experiment. This demonstrates that metapopulation dynamics was not sufficient to promote persistence of the pair of species.

There was little evidence for a difference between treatments in a rescue effect, but treatment had an impact on the coupling of predator and prey dynamics and the spatial coupling of prey dynamics. There was no significant effect of treatment on the minimum ln (prey density + 1) in the predator–prey bottles, indicating that any rescue effect in one treatment did not significantly differ from the effect in the other (Table 3). As in Experiment 1, the lag-zero predator–prey cross-correlation was correlated with persistence (regression equation: Persistence = $76.0 \times r_{pv(0)} + 81.8$; Fig. 3B). This supports the notion that strength of the predator–prey interaction may have influenced persistence. In addition, the average correlation between predator and prey dynamics in the double-predator microcosms was significantly more negative than that in the single-predator microcosms (Table 3). This suggests that the weaker coupling of dynamics in the single-predator microcosms may have enhanced persistence. A larger degree of asynchrony of spatial prey dynamics in the single-predator microcosms may have also enhanced persistence. In the double-predator microcosms, dynamics of the two prey populations were highly correlated (Table 3). Prey dynamics were less synchronous in single-predator microcosms (Table 3).

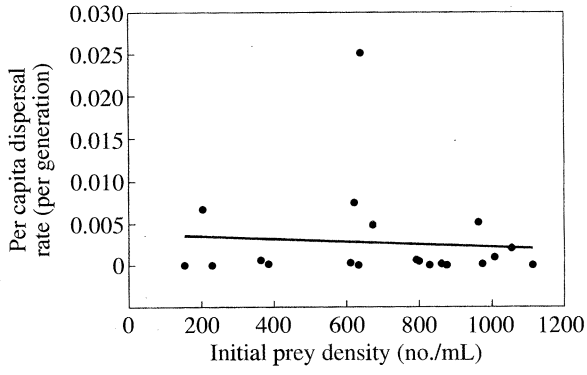


FIG. 6. The relationship between the initial prey density (no./mL) in the bottle in which prey were placed and the proportion that emigrated per generation in Experiment 3. There was no significant relationship between initial prey density and the proportion that emigrated (linear regression, $F_{1,18} = 0.13$, $P = 0.73$). Removal of the outlying point did not yield a linear regression that was significant at $P < 0.05$.

Experiment 3: Dispersal rates

The dispersal experiment yielded an estimate for the per capita rate of prey emigration per generation and a prediction for the long-term prey density of a prey-only bottle from which emigration occurs. The slope of the correlation between the dispersal rate and initial density was not significantly different from zero ($P = 0.725$), hence there was no evidence for density-dependent dispersal (Fig. 6). The mean rate was 0.0027 per generation. The fact that dispersal was density-independent allowed us to replace $e(N)$ with a constant, E, in the model presented above. The model then had an equilibrium prey density of

$$\hat{N} = \frac{k(r - E)}{r}.$$

This led to a predicted long-term density of 237 prey/mL. In fact, the actual mean long-term prey density in the prey-only bottles of the spatial microcosms of Experiment 1 was 75 prey/mL. The ln(density + 1)-transformed value of this latter density is significantly less than the transformed value of the predicted density ($t_4 = -3.62$, $P < 0.05$). This implies that spatial factors other than emigration were largely responsible for the reduction in prey densities in the prey-only bottles when they are members of spatial microcosms.

Discussion

In Experiment 1, predators and prey in spatial microcosms persisted more than three times as long as they did in nonspatial microcosms, showing that spatial dynamics extended persistence. In nonspatial microcosms, predators either drove prey extinct or drove them to an extremely low density and then went extinct themselves (Fig. 1). Predators and prey in nonspatial 60-mL microcosms did not persist any longer than they did in nonspatial 30-mL microcosms (Table 2, Fig. 2A). This demonstrates that enhanced persistence in spatial microcosms was not due to an effect of population or patch size. In fact, enhanced persistence in spatial microcosms appears to be due to a prey rescue effect (Brown and Kodric-Brown 1977). The minimum density to which prey decreased in predator–prey bottles of spatial microcosms was much larger than that of nonspatial microcosms. This indicates that prey dispersed from prey-only bottles to predator–prey bottles, augmenting small prey densities in the latter. These results are consistent with source–sink dynamics of predators and prey, as in the models of Holt (1985, 1993). The dispersal rate in Fig. 6 is also consistent with a prey rescue effect.

The prey-only bottles and the predator–prey bottles of the single-predator microcosms of Experiments 1 and 2 satisfied the definitions of source and a sink patches. In the absence of immigration, the prey never went extinct in the prey-only nonspatial microcosms, suggesting that prey-only bottles served as source patches. The predator–prey bottles of the single-predator spatial microcosms satisfied the broad definition of a sink patch (negative growth rate at equilibrium). On average there was a net flow of individuals each generation from the prey-only bottles to the predator–prey bottles: in both Experiments 1 and 2, the prey-only bottles supported much larger prey populations than the attached predator–prey bottles (Tables 2 and 3) and dispersal was density independent in Experiment 3 (Fig. 6). Since the prey density in the predator–prey bottles did not exhibit a long-term increase, the prey growth rate must have been negative to balance this continual influx of individuals. However, the suitability of the narrow sink definition is more ambiguous due to the stochastic nature of the prey extinctions in the absence of prey dispersal. Although the predators tended to drive prey extinct in the nonspatial predator–prey bottles, predators did not always drive prey extinct before going extinct themselves.

The lag-zero cross-correlation results suggest that dispersal in the spatial microcosms uncoupled the predator–prey dynamics in the predator–prey bottles. A large (in magnitude), negative correlation in the nonspatial microcosms of Experiment 1 implies that as predator density increased, prey density declined. This is consistent with predator and prey densities cycling strongly and asynchronously. In contrast, the relatively small correlation in the spatial microcosms of Experiment 1 is consistent with a much weaker interaction; changes in the density of one species had no predictable effect on the density of the other species. Again in Experiment 2, the cross-correlation coefficient in the nonpersisting double-predator microcosms was significantly larger (in magnitude) than the coefficient in the single-predator microcosms. McCann et al. (1998) have shown that a strong species interaction, defined by a large per capita interaction strength, leads to population cycles and an increased chance of extinction. A weakening of the interaction leads to a stable equilibrium and a decreased chance of extinction. This phenomenon may have occurred in the present research; prey dispersal in single-predator spatial microcosms may have weakened the predator–prey interaction, especially at low prey density when dispersal had a large effect on prey dynamics.

Our research on the dynamics of the spatial single-predator microcosms of Experiments 1 and 2, which resemble most closely the dynamics encapsulated in source–sink theory, point to the potential importance of a factor not typically considered in source–sink studies. In the spatial microcosms of Experiment 1, emigration of individuals from the prey-only bottles could not directly account for the reduction in prey density in prey-only bottles when they are connected to predator–prey bottles. If emigration was directly responsible for the discrepancy, then according to the simple model the density in the prey-only bottles of the spatial microcosms would have been 1 individual/mL smaller than the density observed in the nonspatial 30-mL bottles. However, the difference was much larger, 163 individuals/mL. Notwithstanding the simplicity of the model, the size of the discrepancy suggests that something other than direct emigration influenced dynamics. The removal of nutrients from the prey-only bottles through prey emigration may have influenced dynamics. Alternatively, a toxicant may have diffused from the predator–prey to the prey-only bottles, resulting in a reduction in prey population growth rate or equilibrium abundance. Further investigation would be necessary to confirm either of these and verify their importance to the dynamics.

Our findings support the conclusions of metapopulation studies which typically suggest that immigration, spatially asynchronous dynamics, and rescue effects are important for persistence. We found evidence for asynchrony and rescue effects, hallmarks of classic metapopulation dynamics, in our single-predator spatial microcosms. However, the details by which these mechanisms were achieved in the single-predator spatial microcosms differed from those of classic metapopulation dynamics. The prey-only bottles of the single-predator spatial microcosms were not vulnerable to extinction. The prey densities in the prey-only bottles of the single-predator microcosms were very large (Tables 2 and 3), never approaching zero during the ex-

periment and in isolation (nonspatial prey-only microcosms of Experiment 1) the prey never went extinct. In addition, in microcosms in which both bottles were subject to unstable dynamics (the double-predator microcosms of Experiment 2) the small rate of prey dispersal observed was insufficient to balance the locally unstable dynamics. In contrast, our results are inconsistent with the specific mechanism by which a refuge promotes mathematical stability in ecologists' models. The inverse relationship between total prey density and the proportion of the prey located in the prey-only bottles of the spatial microcosms predicted by refuge theory (Sih 1987) existed in only one of six replicates. In addition, the very small rate of prey dispersal in Experiment 3 (i.e., 0.0027 per generation) suggests that prey resided in two distinct populations, unlike the well-mixed population typical of prey refuge models. The stabilizing mechanism and lack of spatial structure typical of refuge models do not appear to apply to the single-predator spatial microcosms.

Although we were able to obtain a detailed record of spatial dynamics, our experimental design could not circumvent all the traps of studying spatial population dynamics. It was not possible to ensure that both local and regional initial predator–prey ratios remained constant across treatments. For instance, although the ratio in the nonspatial 30-mL bottles was equal to the local ratio of the single-predator spatial microcosms, the regional ratio of the latter was half the ratio of the former (Fig. 2). We predict that if either local or regional initial predator–prey ratio influenced persistence, treatments with small ratios would have consistently persisted longer than treatments with large ratios. We base this prediction on Holyoak and Lawler (1996), who demonstrated for a closely related predator–prey pair (*Didinium nasutum* and *Colpidium striatum*) that an increase in the initial predator–prey ratio caused a decrease in the persistence time. Our results, however, offer no evidence for this (Fig. 2).

This study has demonstrated that a prey source–sink structure enhanced the persistence of interacting predators and prey. In addition, it indicated that nutrient dynamics may have influenced population dynamics. However, this process has not been incorporated into source–sink theory. The complexity of the dynamics observed in this simple system highlights the need for caution in interpreting the dynamics of more complex predator–prey systems in which data are more limited. Multiple processes undoubtedly influence predator–prey persistence and these may be difficult to distinguish with limited experimental data. Structured metapopulation models (reviewed by Gyllenberg et al. 1997) or more simple models, such as transition matrices based on empirically observed relationships between population size and extinction (e.g., C. Ray, A. Hastings, and S. Harrison, *unpublished manuscript*), may be useful for understanding the complex interactions between these local and regional processes.

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