

# Habitat Patch Arrangement and Metapopulation Persistence of Predators and Prey

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**ABSTRACT:** This study tests whether spatial dynamics can stabilize metapopulations with a small number of patches and tests the influence of patch arrangement. I measured persistence of predator and prey protists in replicated microcosms with two to four patches. Predators persisted for 85–437 generations (26–130 d). As predicted by single-species and/or predator-prey metapopulation models, substantial variation in predator metapopulation persistence was accounted for by the amount of patches or habitat, number of dispersal corridors, maximum interpatch distance, and proportion of patches providing colonists (which depends on the explicit spatial arrangement of patches). Contrary to expectation, persistence was not influenced by loops of patches or patch similarity. Persistence was also shorter in four-patch loops than three-patch loops, indicating an interaction between patch number and arrangement, which is not predicted by published models. Spatial synchrony of density fluctuations was central to predator persistence but had complex effects on extinction-colonization dynamics, rescue effects, and predator-prey interaction strength. Levins's model, containing only extinction-colonization dynamics, predicted patch occupancy for prey but not predators. Predators did, however, show rescue effects and changes in interaction strength. This work illustrates the need to combine experimentation with modeling to understand the mechanisms of spatial dynamics.

*Keywords:* metapopulation, persistence, population, predator-prey, rescue effects, spatial synchrony.

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The loss and fragmentation (“breaking apart”) of habitat frequently lead to a reduced number of habitat patches remaining within distances that can be reached by dispersing organisms (Thomas 1994; Harrison 1996). Metapopulation theory proposes mechanisms by which species could persist regionally despite local populations being

small and prone to extinction (Levins 1969). Metapopulations with small numbers of patches are interesting both because of their relevance to conservation and because much of metapopulation theory has come from models with many patches (e.g., Levins 1969; Kareiva 1990; Taylor 1990; Hanski and Gilpin 1997). Consequently, the persistence of small metapopulations remains relatively unexplored. The spatial arrangement of habitat patches is also relevant to metapopulation persistence because it influences the number of adjacent patches that are sources of colonists, the likelihood of interpatch movement, and the degree of independence of dynamics in patches separated by different distances (e.g., Adler and Nuernberger 1994). In this article, I address how the spatial arrangement of a small number of habitat patches and dispersal corridors influences metapopulation persistence of a specialist predator and its prey.

In addressing predator-prey dynamics, metapopulation theory for both single species and predators and prey is potentially relevant. Predators are often emphasized in predator-prey metapopulation studies, and if their effect on prey dynamics is invariant with the arrangement and number of habitat patches, they may be equivalent to a single species feeding on a fluctuating resource. Alternatively, habitat arrangement or predators may alter prey dynamics in ways that make predator-prey theory more appropriate. Here, we consider both kinds of theory because different aspects of dynamics are emphasized by each.

Before considering the effects of habitat patch arrangement, it is useful to consider how the amount of habitat and patch number affect metapopulation persistence. These two factors have separate effects on persistence, although they are frequently confounded (Fahrig 1997, 1998; Bender et al. 1998). A limited amount of habitat can restrict regional population size, which may interact with stochasticity to increase the likelihood of extinction (Fahrig 1997, 1998; Foley 1997; Bender et al. 1998). A limited number of habitat patches can also restrict the potential for metapopulation persistence via a balance between patch extinction and colonization (Levins 1969; Hassell et

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al. 1991; Hanski et al. 1996) or through local populations being rescued from extinction by immigration ("rescue effects"; Brown and Kodric-Brown 1977).

Modeling work shows that the spatial arrangement of small numbers of habitat patches can influence regional persistence. Frank and Wissel (1998) considered classical metapopulations (Levins 1969) of a single species using a stochastic model with five patches of uniform quality and size. By varying dispersal distances and the distance over which extinctions were correlated, they showed that regional persistence was prolonged either by selecting patches that were less likely to go extinct simultaneously or by facilitating recolonization. In the case where individuals could move far enough to reach patches that were more independent in their risk of extinction, persistence was maximized by linear arrays of patches that incorporate greater maximum distances (Frank and Wissel 1998). Patch arrangement can also contribute to regional persistence by facilitating recolonization. Regional persistence should then be maximized by clusters or loops of patches, which provide more local sources of immigrants (leading to rescue, recolonization, and rapid population growth) than linear patch arrangements (Frank and Wissel 1998). This supports and unifies previous theoretical work predicting that increased landscape connectivity (Taylor et al. 1993; Adler and Nuernberger 1994; Fahrig and Merriam 1994) or loops of patches (Lefkovich and Fahrig 1985) enhance regional persistence by maximizing patch recolonization rates.

Apart from the explicit spatial arrangement of patches, patch networks can vary in a number of factors that influence metapopulation persistence of a specialist predator and its prey. These factors have been examined using models with Lotka-Volterra or Nicholson-Bailey dynamics within patches and diffusive dispersal between patches (reviews: Kareiva 1987, 1990; Taylor 1990; Harrison and Taylor 1997; Nee et al. 1997). Simulations with large numbers of habitat patches show that predators and prey persist longer in systems with more patches (and, hence, more total habitat); persistence is longer when within-patch dynamics are more independent in different patches, providing that recolonization is possible (Crowley 1981; Reeve 1988; Kareiva 1990; Comins et al. 1992; Jansen 1995); and the mean rate of interpatch dispersal has complex effects on dynamics. At low dispersal rates of both species, predators go extinct from local patches more frequently than they recolonize, causing regional predator extinction. Either low or high dispersal rates may synchronize dynamics across all patches and allow predators to drive prey regionally extinct (Blasius et al. 1999; Jansen 1999). However, at intermediate dispersal rates, both species may be able to persist through rescue effects and a balance between

patch extinction and recolonization (Crowley 1981; Kareiva 1990; Taylor 1990).

Laboratory experiments can provide valuable tests of metapopulation theory (Nachman 1987a, 1987b; Holyoak and Lawler 1996a, 1996b; Janssen et al. 1997; Gonzalez et al. 1998; Zemek and Nachman 1998; Holyoak, in press). The rapid generation times of the study organisms, the ciliates *Didinium nasutum* and *Colpidium striatum*, allow persistence to be studied directly. The small spatial scale permits construction of replicated patch arrangements. Earlier experiments using these species compared predator and prey persistence and dynamics in subdivided microcosms of nine or 25 patches and the same total amount of undivided habitat (Holyoak and Lawler 1996a, 1996b). In patchy habitats, spatial dynamics extended persistence of the predator by an average of over 200 generations compared to the large undivided populations. This system is, therefore, appropriate to test how other aspects of habitat fragmentation influence persistence.

This article has three related aims. First, I test predictions from the above models about how patch arrangements affect predator and prey metapopulation persistence (specific hypotheses are detailed in the next paragraph). Second, for each species I evaluate how habitat structure influences the relative importance of different metapopulation persistence mechanisms, such as extinction-colonization dynamics (Levins 1969) and rescue effects (Brown and Kodric-Brown 1977). I tested the ability of a simple model containing only extinction-colonization dynamics (Levins 1969) to predict patch occupancy. Both rescue effects and extinction-colonization dynamics are influenced by the degree of correlation between dynamics in different patches, which was also investigated directly. Levins's model also includes no explicit spatial structure and is, therefore, a useful end point, at which the explicit spatial arrangement of patches does not influence dynamics. Third, I explore the potential for dispersal to alter the strength of interaction between predators and prey within patches and the stability (persistence) of local dynamics (Reeve 1988; Rohani et al. 1996; Roland and Taylor 1997; Holyoak et al., in press).

I tested two predictions from Frank and Wissel's (1998) model. First, if patches have semi-independent risks of extinction, patch arrangements that include greater maximum distances should favor regional persistence because patches farther apart tend to have less correlated dynamics (Crowley 1981; Holyoak and Lawler 1996a, 1996b). Second, independent of the first, patch arrangements that make recolonization more likely should facilitate metapopulation persistence. Hence, persistence should be maximized by greater interpatch dispersal rates and patch arrangements with less compartmentalization (defined below). Metapopulation models predict that these effects

should continue until movement rates between patches become high enough to synchronize regional dynamics.

I manipulated the spatial arrangements of groups of two to four interconnected bottles (habitat patches) containing *D. nasutum* and *C. striatum*. Microcosms were constructed to provide independent variation in the number of habitat patches, which co-varies with the amount of habitat (these effects were separated in earlier studies and are not the primary focus of this study; Holyoak and Lawler 1996a, Holyoak, in press; Holyoak et al., in press); the dispersal rate between patches, which was varied by manipulating the number of tubes (corridors) connecting bottles; the maximum distance between patches; whether patches are arranged in loops; and landscape compartmentalization, defined as the percentage of patches directly connected by a corridor (tube) to a chosen target patch; this definition shares much with "connectivity." I avoid the term "connectivity" because of its use as a descriptor of both landscape patterns (interpatch distance) and the dispersal rates of organisms (Fahrig and Merriam 1985; Bradford et al. 1993; Taylor et al. 1993; Clergeau and Burel 1997).

## Material and Methods

### *The Study Organisms*

*Didinium nasutum* is an obligate predator (Laybourn 1977) that feeds mainly in the water column (Berger 1980). Both the prey *Colpidium striatum* and *D. nasutum* divide asexually (Laybourn and Stewart 1974). Under similar experimental conditions to those used here, generation times were  $5.2 \pm 0.1$  SD ( $n = 30$ ) h for prey and  $7.1 \pm 0.1$  ( $n = 8$ ) h for predators when with abundant prey (Holyoak and Lawler 1996a). Predators consumed about 18 prey between divisions (Holyoak and Lawler 1996a). *Didinium nasutum* is capable of forming resting cysts (Beers 1935) but not when reared on *C. striatum*. Ciliate species such as *D. nasutum* and *C. striatum* are patchily distributed at scales of just centimeters in ponds (Taylor and Berger 1980). In microcosms with bottles connected by a single tube (corridor) in the same way as this study, per generation dispersal rates were 0.5%–2.5% of individuals for prey and 0.08%–24.8% for predators (depending on food availability; Holyoak and Lawler 1996a, 1996b).

*Colpidium striatum* shows logistic growth in the absence of predators and does not drive its bacterial prey extinct or become extinct itself in the absence of predators if small volumes of nutrient medium are replaced periodically (e.g., Morin and Lawler 1996). *Didinium nasutum* and *C. striatum* were, therefore, treated as a predator-prey system (rather than as a three-level system including the bacteria) as other authors have done with *D. nasutum* and *Para-*

*mecium* species (Gause [1934] 1964; Luckinbill 1973; Salt 1974; Maly 1978; Hewett 1980).

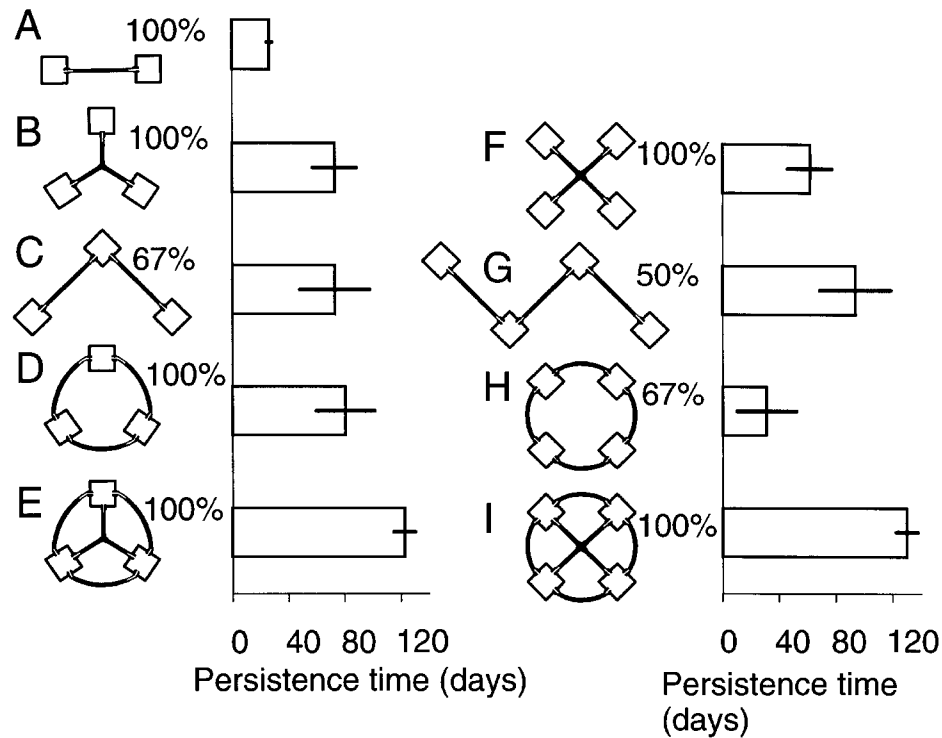
### *Microcosms, Setup, and Sampling*

I created nine different arrangements of linked bottles (arrays), with four replicate microcosms per arrangement (fig. 1). Arrays consisted of 32-mL polypropylene bottles connected by silicon rubber tubes of 3.2-mm internal diameter. Tubes were 11.2 cm long except in microcosms E and I (fig. 1), where curved tubes of 12.2 and 11.0 cm were used because of geometric constraints; these small differences in tube lengths were ignored in statistical analyses. Each tube was attached to a bottle using a connector of 2-mm internal diameter, which displaced a volume of 0.9 mL from the bottle and which was contained in the tube. The wall surface area of microcosms necessarily changed with the number of tubes per bottle. However, the species used feed mainly in the water column and were not influenced by surface area in previous experiments (Holyoak and Lawler 1996a, 1996b).

The experiment was started by filling bottles with 30 mL of sterilized nutrient solution made from one Protozoan Pellet (Carolina Biological Supply, Burlington, N.C.) in 1 L of 50 : 50 spring : distilled water. Approximately 40 *C. striatum* and associated bacteria from the *C. striatum* culture were added per milliliter of nutrient solution. Two days later, four *D. nasutum* were added to every bottle, and thereafter, densities were sampled every 2 d for the first 74 d. Samples of 3 mL were taken from individual bottles after tightening bottle caps to minimize between-bottle flow. *Colpidium* were counted in a five-drop (0.032 mL/drop) subsample and predators were counted in the entire 3 mL. Samples were replaced with fresh sterile nutrient medium, which created a semicontinuous batch culture. After day 74, samples were still replaced regularly, but presence/absence checks were performed only on every fifth sample period (every 10 d), and other samples were discarded. Individual microcosms were discarded when predators were entirely absent for five consecutive samples; earlier experiments in which entire bottle contents were checked showed that this procedure reliably indicated predator extinctions (Holyoak and Lawler 1996a). The experiment was ended on day 130, which was arbitrarily chosen. All microcosms were kept at room temperature ( $\bar{X} = 23^\circ\text{C}$ ).

### *Statistical Methods*

A one-way ANOVA was used to test whether the number of patches (or total amount of habitat) influenced predator persistence in all microcosms. A second ANOVA, restricted to three- and four-patch microcosms, tested the effect on



**Figure 1:** Mean predator persistence and microcosm structure. Figures beside bars give compartmentalization, the mean percentage of other bottles directly connected by tubes averaged across all bottles in each microcosm. Error bars are  $\pm 1$  SE. Persistence is unknown for predator populations that did not go extinct but was assumed to be 130 d, the duration of the experiment.

predator persistence of interpatch dispersal rate, maximum interpatch distance, landscape compartmentalization, and loop formation of patches and tubes. Excluding two-patch microcosms allowed more interaction terms to be included, and this was necessary for the ANOVA to give similar results to comparisons of pairs of microcosms that varied in a single factor. Factors in this second ANOVA were the number of patches (three or four), mean number of tubes per bottle (1, 1.33, 1.5, 2, or 3), whether patch arrangements were compartmentalized (i.e., <100% of patches were linked directly by tubes), whether there was a strict loop structure (microcosms D and H; fig. 1), and the maximum distance between patches (1, 2, or 3 tubes). When distances ( $d$ ) were greater than one tube (microcosms C, G, and H; fig. 1), there were also  $d - 1$  bottles separating bottles. Preliminary analyses also considered a factor that coded for whether all patches within microcosms were identical in their number of connecting tubes. This allowed for the fact that different patches might generate different population sizes, such as in mainland-island models (Boorman and Levitt 1973). However, I found no significant effects of the similarity of patches, and for simplicity, I removed this factor from ANOVAs.

The degree of independence of density fluctuations in different bottles (spatial synchrony) was measured using the lag-zero cross correlation (Hanski and Woivod 1993) calculated from either  $\ln$ -transformed prey or predator densities. For prey, the cross-correlation coefficient was termed  $r_{x,x'(0)}$ , where  $x$  represents a series of  $\ln$ (densities) from one bottle and  $x'(0)$  is an unlagged  $\ln$ (density) series from another bottle within a microcosm (see Box and Jenkins 1976 for formulas). Equivalently, the lag-zero cross-correlation coefficient for predators was  $r_{y,y'(0)}$ .

I also calculated the cross correlation ( $r_{x,y(k)}$ ) between predator densities,  $y(k)$ , and prey densities,  $x$ , within bottles as a measure of the "interaction strength" between predators and prey. Lags ( $k$ ) of  $-3$  to  $+3$  ( $-6$  to  $+6$  d) were calculated using  $\ln$ (density + 1) transformed series. This quantifies the average correlation between predator and prey densities through time and across all densities that occurred. I excluded the initial densities when the species were introduced to microcosms and standardized series to 11 samples, spanning 22 d until extinction of the first microcosm. For simplicity, all  $r_{x,y(k)}$  values discussed hereafter refer to  $k$  values that maximized the absolute value of  $r_{x,y(k)}$ .

**Table 1:** ANOVA of predator persistence in three- to four-patch microcosms

Factor	Sum of squares	df	Mean square	<i>F</i>	<i>P</i>	Variance (%)	Effect size <sup>a</sup> (d)
Compartmentalization ( <i>C</i> ) <sup>b</sup>	6,235	1	6,235	6.09	.02	9.2	28.8
Tubes per bottle	24,307	4	6,077	5.93	.002	35.9	71.8
Patches ( <i>P</i> )	465	1	465	.45	.51	...	...
Maximum distance	10,555	2	5,278	5.15	.01	15.6	42.3
Loop structure ( <i>L</i> ) <sup>c</sup>	1,650	1	1,650	1.61	.22	...	...
<i>P</i> × <i>C</i>	508	1	508	.49	.49	...	...
<i>P</i> × <i>L</i>	3.1	1	3.1	.01	.96	...	...
Error	26,623	26	1,024	...	...	...	...

Note: Persistence did not differ from normality in a  $\chi^2$  test ( $P = .4$ ), and variances were homogeneous in a Bartlett's test ( $P = .6$ ).

<sup>a</sup> Effect size is the maximum difference between mean persistence for each factor.

<sup>b</sup> Compartmentalization indicates whether all patches were directly connected by corridors or not (fig. 1).

<sup>c</sup> Loop structure indicates whether patches formed a strict loop, which it does in types D and H.

I used Levins's (1969) metapopulation model as a null model to test whether observed patch occupancy could be explained by observed patch extinction and colonization rates. This model assumes that fixed extinction and colonization rates lead to an equilibrium level of patch occupancy. Discrepancies between this model and experiments might indicate that regional persistence is driven by factors not included in the model or that patch occupancy is not at equilibrium. Levins's (1969) model predicts patch occupancy  $\hat{p} = 1 - (e/c)$ , where extinction probability,  $e$ , was estimated as the proportion of occupied patches (32-mL bottles) becoming extinct between samples (at 2-d intervals) and was averaged for all times and all bottles within each microcosm. Similarly,  $c$  was estimated for each microcosm as the proportion of unoccupied patches that were colonized within a time step of 2 d. A potential problem with this analysis is that not all recorded zero densities represent real extinctions and that an extinction followed by a recolonization within a 2-d period would have been overlooked in samples at 2-d intervals. However, these forms of sampling error should increase both  $e$  and  $c$ , and consequently, the ratio  $e/c$ , which is used to calculate patch occupancy, should not be strongly influenced by these forms of sampling error.

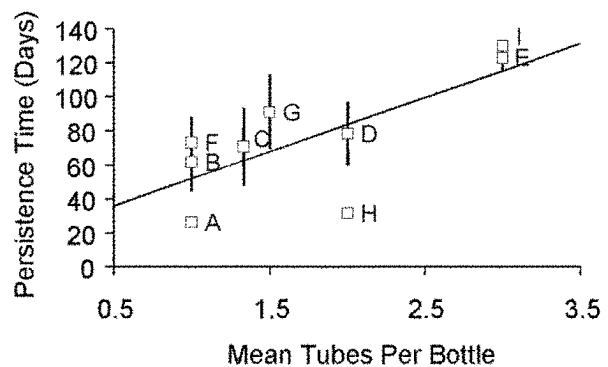
## Results and Discussion

### Effects of Patch Arrangement

The average persistence of predators varied from 26 to 130 d (about 85–437 predator generations; fig. 1). Despite this fivefold variation, predator persistence times were highly predictable using habitat features that are expected to be important based on their effects in single-species and predator-prey metapopulation models. Altogether, three habitat factors explained 61% of variance in predator persistence in three- to four-patch microcosms (table 1), and

in a separate analysis, the difference between two versus three or four patches explained 15% of variance in predator persistence. Prey did not go extinct from any microcosm.

As predicted by a single-species model (Frank and Wissel 1998), increasing the maximum distance between patches (bottles) extended predator persistence (by up to 42 d; table 1). Patches that were farther apart also had lower spatial synchrony, indicated by the lag-zero cross correlations for prey,  $r_{x,x'(0)}$ , and predators,  $r_{y,y'(0)}$ . These effects are best illustrated by microcosms C and G, which contain the greatest maximum distance. In these microcosms, a linear regression of the mean prey cross correlation for each distance in each microcosm ( $\bar{r}_{x,x'(0)}$ ) against distance between bottles had a slope of  $-0.083$  (SE = 0.023,  $t = -3.69$ ,  $df = 18$ ,  $P < .002$ ,  $R^2 = 0.43$ ; intercept = 0.90, SE = 0.04). Analogous results were

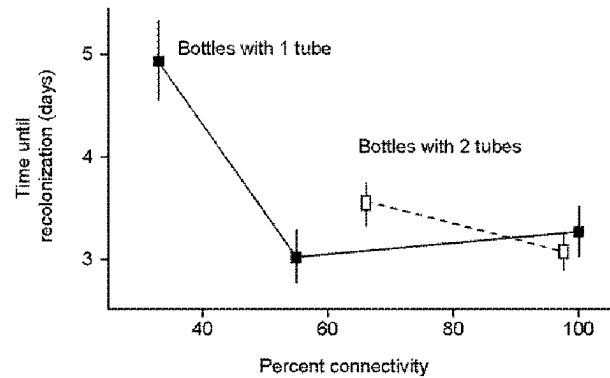


**Figure 2:** Effect of mean tubes per bottle on predator persistence in different kinds of microcosms, indicated by letters on the graph. Bars show the mean  $\pm$  1 SE, and error bars are too small to see in some cases. Line is from a linear regression (see text).

obtained for predators (slope =  $-0.091$ , SE =  $0.025$ ,  $t = -3.71$ ,  $df = 18$ ,  $P < .002$ ; intercept =  $0.67$ , SE =  $0.03$ ). Spatial synchrony of density fluctuations is also central to persistence in predator-prey metapopulation models (Crowley 1981; Reeve 1988; Nisbet et al. 1992; Jansen 1995).

Consistent with both single-species models (Taylor et al. 1993; Fahrig and Merriam 1994; Frank and Wissel 1998) and predator-prey metapopulation models (Crowley 1981; Reeve 1988; Kareiva 1990; Comins et al. 1992), predator persistence increased with dispersal (Pearson's  $r = 0.57$ ,  $n = 36$  microcosms,  $P < .001$ ; fig. 2). Dispersal rate, manipulated by changing the number of tubes per bottle, accounted for 36% of variance in predator persistence in an ANOVA and produced up to 72 d difference in mean persistence (table 1; fig. 2). Microcosms A (with only two patches) and H (with a loop structure) were exceptions to this pattern (fig. 2) but also fit with the theory for predator-prey metapopulations (see below).

As predicted by Frank and Wissel (1998), regional persistence was longer when habitats were not compartmentalized so that a greater proportion of patches could provide colonists (fig. 1; table 1). For three- to four-patch microcosms, mean predator persistence was 93 d with all patches interconnected (SE =  $9.1$ ,  $n = 20$ ; fig. 1B, 1D–1F, 1I) but only 64 d (SE =  $12.3$ ,  $n = 12$ ) in compartmentalized habitats (fig. 1C, 1G, 1H). This is the first experimental demonstration that metapopulation persistence is influenced by the explicit spatial arrangement of patches and corridors, as opposed to nonspatial scaling factors like mean dispersal rate. Frank and Wissel (1998) also predicted that compartmentalization would alter the length of local extinctions (within individual patches). Here, predator extinctions were indicated by zero densities, which were recorded from 21%–40% of 3-mL samples, depending on the microcosm (Holyoak, in press, showed that 55% of such zero densities represent predator extinctions; in this experiment, local extinctions of prey were recorded in only 0%–2% of samples). Patches connected to a larger proportion of patches within microcosms (lower habitat compartmentalization) were recolonized by predators more quickly (fig. 3). This effect was significant in a one-way ANOVA for bottles with one tube ( $F = 6.74$ ,  $df = 2, 13$ ,  $P < .01$ ), but not two tubes ( $F = 5.21$ ,  $df = 1, 14$ ,  $P < .5$ ). Both of the effects of compartmentalization are congruent with a single-species model that varied the spatial distribution of patches (Adler and Nuernberger 1994). Their work showed that compared to clumped patches, randomly distributed patches produced shorter metapopulation persistence times and longer times to patch recolonization. However, Adler and Nuernberger's model focused on local population size, and it is not clear whether differences in persistence and time until recolo-



**Figure 3:** Mean time (d) after recorded extinction until predators recolonized individual 32-mL bottles with various levels of compartmentalization. Compartmentalization was calculated separately for different bottles and is not the microcosm average as in figure 1. One-way ANOVA tested for differences in recolonization periods separately for bottles with one and two tubes; a  $\chi^2$  test checked normality, and a Bartlett's test checked homogeneity of variances before analysis. Bars show standard errors.

nization were caused by differences in the mean rate of interpatch dispersal, which also varied with the spatial distribution of patches. Here, mean dispersal rate was controlled separately by altering the number of tubes per bottle.

Correlations between spatial synchrony and predator persistence provided evidence for spatial dynamics extending persistence in all microcosms except types A and H, where predator persistence was short (fig. 2). Consistent with predator-prey metapopulation models, persistence increased with increases in dispersal opportunities until the point where density fluctuations across patches became synchronous (Crowley 1981; Reeve 1988; Nisbet et al. 1992; Jansen 1995). In microcosms A and H, mean prey lag-zero cross correlations between adjacent bottles were high, indicating synchrony ( $\bar{r}_{x,x(0)} = 0.91$ – $0.93$ , SE =  $0.01$  per microcosm type); dynamics in other types of microcosm were less synchronous (equivalent figures were  $\bar{r}_{x,x(0)} = 0.78$ – $0.84$ , SE =  $0.01$ – $0.04$ ). In microcosms A and H, density plots also showed that prey densities crashed synchronously in all bottles at the end of the first predator-prey cycle, causing predators to starve to death in all bottles. Conversely, in other microcosms, there was typically a 2-d variation between bottles in the timing of prey density crashes. Such variation could have permitted some predators to survive by moving to patches where prey were still abundant.

In an ANOVA including all microcosms, the amount of patches or habitat produced up to 61-d difference in the mean persistence per microcosm type ( $F = 6.27$ ,  $df =$

2, 27,  $P < .01$ ; 15% of variance was explained). Least significant difference tests on means indicated that this was because of two-patch microcosms' having shorter persistence than three- or four-patch microcosms (figs. 1, 2), but the latter did not differ from each other (at  $P < .05$ ). Such an effect is predicted by models with either a limited total population size or with a limited number of patches, and this analysis does not attempt to separate these effects (Fahrig 1997, 1998; Foley 1997; Bender et al. 1998).

In contrast to the single-species model of Lefkovich and Fahrig (1985), I found no independent effect of loop structures of patches (present in microcosms D and H) on predator metapopulation persistence (table 1; fig. 1). A power test indicated that nine replicates of an otherwise identical loop and nonloop arrangement of patches are required for an 80% chance of detecting a 1 SD (equivalent to 41 d) difference in persistence at  $P < .05$  in the ANOVA. Given that three other factors with effect sizes of  $< 41$  d were shown to influence regional persistence, this indicates a minor effect of loop structure on persistence. A likely explanation is that in Lefkovich and Fahrig's model, extended persistence in loops of patches over linear patch arrangements was caused by compartmentalization. These authors did not consider the effect of compartmentalization because it had not yet been described.

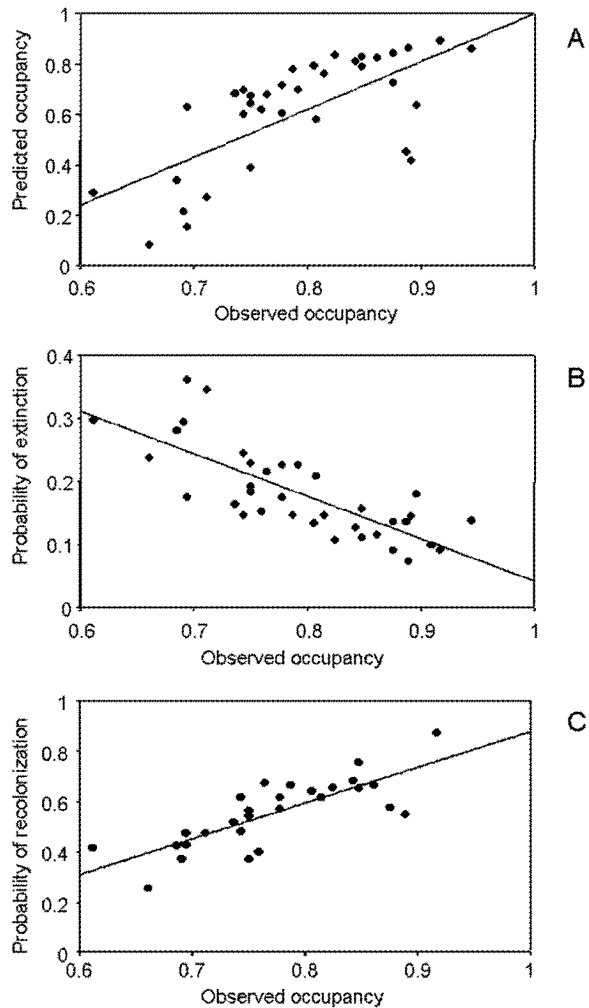
A puzzling anomaly is that in microcosms with a strict loop of patches, predators on average persisted for 47 d fewer in microcosms with four (H) patches than with three (D) patches ( $31 \pm 3.1$  d [ $\pm$ SE] vs.  $78 \pm 18.9$  d; Student's  $t = 2.45$ ,  $df = 6$ ,  $P < .05$ ; fig. 1). A suite of statistics also differed between these microcosm types: First, predators had a 47% higher peak density in H than in D ( $5.91 \text{ mL}^{-1}$  vs.  $4.02 \text{ mL}^{-1}$ ; Student's  $t = 1.98$ ,  $df = 6$ ,  $P < .05$  in a one-tailed test). Second, both predator and prey dynamics in adjacent patches were more synchronous in H than D; for prey  $\bar{r}_{x,x(0)} = 0.91$  and  $0.84$  for H and D, respectively, Student's  $t = 5.43$ ,  $df = 6$ ,  $P < .002$ , and  $\bar{r}_{y,y(0)} = 0.68$  and  $0.51$ ,  $t = 2.84$ ,  $df = 6$ ,  $P < .05$ , for predators. Third, the average correlation between predator and prey densities through time within a 32-mL bottle was more strongly negative in H than D ( $\bar{r}_{x,y(k)}$  mean correlation =  $-0.77$  and  $-0.44$ , respectively,  $t = 4.34$ ,  $df = 6$ ,  $P < .005$ ); this is consistent with a stronger predator-prey interaction (across all densities and averaged through time) within bottles of microcosms H than D. Altogether, six dependent variables were tested for differences between microcosms D and H, and overall differences were significant in a MANOVA (Wilks's  $\lambda_{6,1} = 0.00044$ ,  $P < .05$ ). These results suggest a possible interaction between patch number and arrangement, which occurred despite microcosms being initiated under identical conditions. Results were also homogeneous across replicates. No published model of which I am aware pre-

dicts such an interaction. However, models of predator and prey metapopulations (similar to those considered by Crowley 1981; Reeve 1988; Hassell et al. 1991) do predict similar changes in dynamics when dispersal is manipulated. It would be interesting to test whether the experimental results are repeatable and how a wider range of patch numbers (or spatial scales) influence persistence in loops of patches. Explaining these results represents an interesting theoretical challenge, which requires the use of models with an explicit spatial arrangement of patches.

#### *Dynamical Mechanisms of Metapopulation Persistence*

There are a variety of mechanisms by which predators and prey could persist regionally. Metapopulation persistence mechanisms include rescue effects, extinction-colonization dynamics, spatial independence of dynamics, patch size effects, habitat-specific demography, and habitat dynamics. Holyoak and Ray (1999) suggest studying these mechanisms directly rather than classifying metapopulations according to theoretical "types" (source-sink, classical metapopulation, mainland-island, etc.). Classification belies the fact that real systems may be intermediate between types (Harrison and Taylor 1997). For predator-prey interactions, it is complex to identify mechanisms because habitat features may directly influence prey or predator dynamics and the strength and stability of the predator-prey interaction. One way to make progress is to test whether observed dynamics can be predicted using a null model, such as the Levins's (1969) model, which includes only extinction-colonization dynamics.

For predators, Levins's model underestimated observed patch occupancy in all but two of 36 microcosms (fig. 4A). The size of the discrepancy varied from 6% in microcosms of types B and I, to 36% in microcosm H. Predator persistence was longer in microcosms where observed patch occupancy exceeded predicted occupancy by greater amounts (Pearson's  $r = 0.66$ ,  $P < .001$ ), and prey or predator dynamics across patches (indicated by  $r_{x,x(0)}$  and  $r_{y,y(0)}$ ) were less synchronous (Pearson's  $r = -0.47$  and  $-0.41$ ,  $P < .005$  and  $P < .02$ , respectively). This asynchrony and extended persistence was associated with at least three effects not predicted by Levins's model. First, rescue effects were suggested by a strong negative correlation between the observed probability of predator extinction from a 32-mL bottle and the proportion of bottles occupied (fig. 4B; Pearson's  $r = -0.77$ ,  $n = 36$ ,  $P < .001$ ). Second, the probability of 32-mL bottles being recolonized by predators was positively correlated with the proportion of bottles occupied (fig. 4C;  $r = 0.79$ ,  $n = 28$ ,  $P < .001$ ; excluding eight microcosms where  $c$  could not be accurately assessed because  $< 5$  recolonizations occurred). Third, the probability of predators recolonizing



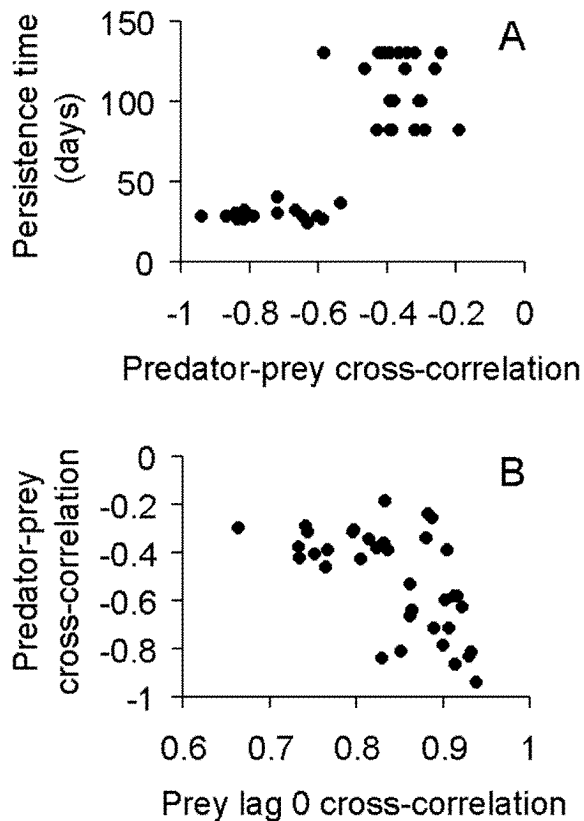
**Figure 4:** Occupancy, extinction, and recolonization probabilities (per 2 d) for predatory *Didinium nasutum*. A, Predicted proportion of patches occupied per microcosm calculated from Levins's (1969) model plotted against the observed proportion of patches occupied (Pearson's  $r = 0.85$ ,  $P < .001$ ). B, Probability of extinction and recolonization (C) of local predator populations in 32-mL bottles plotted against observed occupancy.

bottles was also weakly correlated with average predator density in occupied bottles ( $r = 0.36$ ,  $n = 28$ ,  $P \approx .05$ ). The presences of these factors is consistent with them contributing to the discrepancy between predicted and observed occupancy and, hence, to prolonging regional persistence. It therefore seems unlikely that the assumption of an equilibrium between patch extinction and colonization (Levins 1969) is the reason for the limited success of the null model. However, further analyses would be required to clarify how much each mechanism contributes to regional persistence.

In contrast to predators, observed patch occupancy for prey was accurately predicted by equilibrium extinction-colonization dynamics. Mean patch occupancy ( $\hat{p}$ ) predicted from extinction-colonization dynamics was virtually identical to observed occupancy (98.67% vs. 98.71% of patches, respectively; prey occupied 94%–100% of bottles, the mean probability of extinction was 0.012 per 2 d, and the probability of recolonization was 0.963 per 2 d). Across microcosms, predicted and observed occupancy were also strongly correlated (Pearson's  $r = 0.987$ ,  $n = 20$ ; excluding 16 microcosms with  $< 5$  recolonization events). Despite the ability of extinction-colonization dynamics to explain patch occupancy, rescue effects were also found; there was a strong correlation between the probability of extinction from a bottle and the proportion of bottles occupied ( $r = -0.985$ ,  $n = 36$ ,  $P < .001$ ). Hence, although rescue effects were evident, they did not appear to set patch occupancy. Consistent with this, there were significant ( $P < .05$ ) correlations between prey abundance in occupied patches and the likelihood of local extinction of prey (also indicating rescue effects); predator occupancy, and the strength of the predator-prey interaction (described in the next paragraph). Hence, prey abundance within occupied patches is influenced by, and influences, many aspects of the predator-prey interaction and is not a clear indicator of prey rescue effects. Furthermore, the success of Levins's model at predicting prey occupancy suggests that although other factors are present, they do not appear to be driving patch occupancy.

Regional persistence times were longer when within-patch predator-prey interactions were weaker (when  $r_{x,y(k)}$  was less strongly negative during the first 22 d after predator introduction; Pearson's  $r = 0.80$ ,  $P < .01$ ,  $n = 36$ ; fig. 5A). Consistent with this, theory suggests that spatial structure can stabilize spatial predator-prey systems by limiting the predators' attack rate on the prey (Kareiva 1990; Murdoch 1994). An association between persistence and per capita interaction strength was also predicted for community modules of three or four species in nonspatial models (McCann et al. 1998). However, it should be noted that McCann et al. used per capita interaction strength, defined as the net per capita effect of one species on the density of another. Furthermore, although per capita interaction strength is easily defined theoretically (McCann et al. 1998), its measurement is likely to depend on experimental conditions and the properties of the selected metric (Berlow et al. 1999). It would be useful to explore the statistical properties of the selected cross-correlation coefficient to clarify what it measures and how this is related to commonly used predator-prey models.

Interestingly, there was also a strong correlation between within-patch predator-prey interaction strength,  $r_{x,y(k)}$  and the degree of spatial synchrony of prey density fluctuations,



**Figure 5:** *A*, Influence of the strength of predator-prey coupling on predator persistence. Strength of coupling was measured using the maximum cross correlation between ln-transformed predator and prey densities within bottles. Predators lagged prey by 2–6 d. Each point is a microcosm mean. *B*, Relationship between predator-prey coupling (predator-prey cross correlation) and spatial synchrony in prey density fluctuations across patches (prey lag-zero cross correlation). Each point is a microcosm mean based on randomly selected pairs of bottles for the prey lag-zero cross correlation.

$r_{x, x(0)}$  (Pearson's  $r = -0.60$ ,  $P < .02$ ,  $n = 36$ ; fig. 5*B*). Hence, asynchronous density fluctuations were associated with weaker predator-prey interactions and longer predator persistence. While some regard the study of asynchrony as trivial and uninformative (de Roos and Sabelis 1995), we should bear in mind that asynchrony is a prerequisite for metapopulation persistence through either rescue effects (Brown and Kodric-Brown 1977) or extinction-colonization dynamics; if all patches declined to low abundances simultaneously, there would be no source of migrants that are the agents of recolonization and rescue.

Like a simple metapopulation model (Hanski and Gyllenberg 1997), spatial dynamics produced a positive distribution-abundance relationship for predators and prey; Pearson's correlations between the proportion of patches

occupied and mean abundance in occupied patches was  $r = 0.64$ ,  $P < .001$  for predators and  $r = 0.66$ ,  $P < .001$  for prey. Gonzalez et al. (1998) also found a similar relationship in arthropod communities in artificially fragmented habitats and showed that habitat fragmentation reduced both distribution and abundance. In this study, greater occupancy of predators was also associated with longer persistence (described above). Although such relationships are potentially useful, we need to bear in mind that they may have multiple causes, which include mechanisms of spatial dynamics such as rescue and stochastic extinction and colonization (Hanski and Gyllenberg 1997). In multispecies systems, it is also possible that some species decline in abundance during fragmentation because their predators or competitors increase in abundance.

The patterns between persistence and dynamical mechanisms described here are necessarily correlative, but mathematical models could help to identify cause and effect. In choosing model formalisms, great care is required to ensure that different dynamical mechanisms are not subsumed, which hinders the study of the contribution of different mechanisms to regional persistence (Holyoak and Ray 1999). Structured metapopulation models are potentially a powerful tool for assessing the contribution of different mechanisms to persistence (reviewed by Gyllenberg et al. 1997), but they have not been widely used to date, possibly because of their complexity. Simulation models are also powerful tools for investigating different facets of habitat fragmentation, such as the effects of different patch arrangements (e.g., Lefkovich and Fahrig 1985; Frank and Wissel 1998); like experiments, simulation models require the use of carefully planned comparisons to distinguish between persistence mechanisms. Simpler strategic models, which have a minimal amount of detail about population dynamics, can also be useful; for example, factors like population size might be able to be reduced to distributions of probabilities of persistence for each population size. Preexisting models with a single persistence mechanism can also be used as null models, such as this usage of Levins' (1969) model. This list is obviously not exhaustive but is intended to give some ideas about some of the more accessible tools for studying persistence mechanisms. It is also noteworthy that despite studying a predator-prey interaction of a kind that has shaped predator-prey theory (e.g., Gause [1934] 1964), several single-species models gave useful insights into dynamics. We therefore should not constrain ourselves to using multi-species models to test ideas about multispecies systems.

## Conclusions

In conclusion, this experiment shows that habitat patch arrangement can profoundly influence predator and prey

metapopulation persistence. Consistent with single-species and/or predator-prey models, there were substantial effects on predator metapopulation persistence of the amount of patches or habitat, maximum distance between patches, average interpatch dispersal rate, and degree of interconnection of patches; this effect of habitat compartmentalization is the first demonstration that the explicit spatial arrangement of patches influences metapopulation persistence. Despite model predictions, no separate effect was found for loop structures of patches or patch similarity. Also, contrary to expectation, predator persistence was longer in loops of three patches than four patches, which indicates an interaction between patch number and arrangement. This is not predicted by published models of which I am aware. Spatial synchrony of dynamics in different patches was central to persistence. However, its effects were complex because it was correlated with extinction-colonization dynamics, rescue effects, and the strength of predator-prey coupling, which might alter the propensity for within-patch persistence. Using Levins's model as a null model demonstrated that prey patch occupancy was explicable solely by extinction-colonization dynamics. However, additional factors were needed to explain predator patch occupancy. Rescue effects and relationships between recolonization probability and patch occupancy were identified as candidate mechanisms. This work highlights the need for cautious application of mechanistic models and experimentation to identify metapopulation persistence mechanisms.

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