METAPOPULATION EXTINCTION IN FRAGMENTED LANDSCAPES: USING BACTERIA AND PROTOZOA COMMUNITIES AS MODEL ECOSYSTEMS

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Abstract.—Extinction is notoriously difficult to study because of the long timescales involved and the difficulty in ascertaining that extinction has actually occurred. The effect of habitat subdivision, or fragmentation, on extinction risk is even harder to study, as it requires copious replication of habitat patches on large spatial scales and control of area effects between treatments. I used simple small-scale communities of bacteria and protozoa to study extinction in response to habitat loss and habitat fragmentation. I studied several different community configurations, each with three trophic levels. Unlike most metapopulation studies (experimental as well as theoretical), which have tended to deal with inherently unstable species interactions, I deliberately used community configurations that were persistent in large stock cultures. I recorded the time to extinction of the top predator in single habitat patches of different sizes and in fragmented systems with different degrees of subdivision but the same amount of available habitat. Habitat loss reduced the time to extinction of isolated populations. Fragmented systems went extinct sooner than corresponding unfragmented (continuous) systems of the same overall size. Unfragmented populations persisted longer than fragmented systems (metapopulations) with or without dispersal corridors between subpopulations. In fact, fragmented systems where the fragments were linked by dispersal corridors went extinctly significantly sooner than those where subpopulations were completely isolated from each other. If these results extend to more "natural" systems, it suggests a need for caution in management programs that emphasize widespread establishment of wildlife corridors in fragmented landscapes.

It is widely recognized that habitat loss—the reduction of the habitat area available to a focal species—greatly reduces its expected time to extinction. However, it is not well understood how the time to extinction will change if the remaining habitat is distributed across a set of smaller, isolated patches instead of being left in one single continuous tract. It does not follow from the reduced persistence in small patches that a single large population will persist longer than an aggregate set of several smaller populations (with the same total size). To estimate the overall persistence time, or the probability of extinction as a function of time, for a set of populations, one would need to know the entire distribution of extinction times for a single population and the correlation structure of disturbances (and population dynamics) among patches. Moreover, to

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compare a single large habitat patch with several small patches, one must consider not the expected persistence time for each of the small ones but the maximum persistence time for the whole set.

If the distribution of extinction times has a long right tail, such as the geometric or the gamma distributions, it is quite conceivable that the "redundancy" in a set of small patches may more than compensate for their shorter mean extinction times. If extinction is a Poisson process with a constant rate, the times to extinction would be expected to be geometrically distributed. Several authors have reported geometrically distributed extinction times (negative exponential distributions in continuous time) from their analyses of density-dependent stochastic birth-death processes (Tier and Hanson 1981; Goodman 1987; Gabriel and Bürger 1992). Apart from these findings, we know little of the distribution of extinction times in natural populations.

Demographic stochasticity in finite populations causes populations in a set of small remnant patches (a fragmented system) to be more prone to extinction than populations in a large remnant patch (an unfragmented/continuous system) with the same total area (Burkey 1989, 1995a). This suggests that we may minimize loss of biodiversity by minimizing the degree to which we fragment natural habitats. Nature reserves should be as large and unfragmented as possible. On the other hand, forest fires, epidemics, drought, invasion by "exotic" species, and other environmental disturbances may greatly reduce the persistence of populations in single continuous habitat tracts (Goodman 1987; Shaffer 1987; Mangel and Tier 1993). By "not putting all the eggs in the same basket," one may be better able to reduce the rate of species loss from nature reserves in the face of environmental disturbances, catastrophes, and disease outbreaks. Environmental stochasticity and "random" catastrophes may be able to counteract the effect of demographic stochasticity and may potentially render populations in fragmented systems less vulnerable to extinction than populations in continuous systems—provided these disturbances are sufficiently severe and spatially uncorrelated enough (Goodman 1987; Burkey 1989). Whether they do or not is an empirical question, the answer to which may depend on the organism in question, the relative spatial scale of the fragments, and the scale, intensity, and spatial correlation of environmental variability.

A limited area imposes negative density dependence in demographic rates at the population level (even if it is just a simple cap on total population size). In some simple models with negative density dependence, demographic stochasticity produces such nonlinear relationships between available area and persistence that populations in a set of small patches are more vulnerable than populations in single large patches of the same total size (Burkey 1989, 1995a). In a fragmented landscape, bounds (imposed by restricted movement and density dependence within patches) are put on subpopulations at the level of each patch and the added restrictions on subcomponents of the population as a whole cause a reduction in overall viability. I expected such bounds to have similar effects in predator-prey systems and food webs as in single species systems, though some complications exist (Burkey 1995a).

Some models and certain verbal arguments suggest that persistence times of

fragmented systems may be enhanced if forest fragments and nature reserves can be linked with dispersal corridors (Diamond 1975; Wilson and Willis 1975; Brown and Kodric-Brown 1977; Goodman 1987; Burkey 1989, 1993b, 1995a; but see Simberloff et al. 1992; Hess 1994). Thus extinct local populations can be recolonized from within the system and some local extinctions can be avoided through a supplement of individuals from adjacent patches (the "rescue effect"; Brown and Kodric-Brown 1977). Based on a simulated birth-death process model, Goodman (1987, p. 33) suggests that "multiple reserves are preferable to the single large reserve, provided the environmental variation in the separate multiple reserves is at least partially independent, and provided there is at least a small rate of natural or managed recolonization of reserves which experience local extinction." Whether the severity of environmental variation and their spatial correlation structure is such that this holds true must be tested empirically in biological systems. Moreover, it is possible that the spread of disease through dispersal corridors may counteract one of the perceived advantages of fragmented systems (Hess 1994). Further study may suggest other reasons to question the wisdom of relying on reserve systems consisting of small fragments linked by dispersal corridors over large continuous habitat tracts. In general, the recommendations for reserve design suggested by Diamond (1975) and Wilson and Willis (1975) have still not been adequately tested.

Most of the existing metapopulation theory is hard to apply to questions involving extinction risk in fragmented landscapes because of the difficulty of scaling between patches of different sizes. The classical metapopulation models tend to compare single patches and sets of linked patches of indeterminate size (e.g., Levins 1969; Crowley 1981; Renshaw 1991). They may look at predator-prey systems with mutliple populations, but they make no attempt to compare systems across scales and, hence, can say little about effects of habitat fragmentation. Encounter rates, for example, must be scaled in a reasonable manner to reflect changes in the number of prey and predator individuals in patches of different sizes (see de Roos et al. 1991; Burkey 1995a). Studying the effect of (initial) population size, or population density, in an area of indeterminate size is no substitute for studying the effect of area per se.

Most theory in this area has dealt only with single species models (but see Holt 1997, and references therein, for a treatment of deterministic patch occupancy models of food webs and communities in a patchy landscape). Patch occupancy models are tractable but may be misleading since they do not explicitly incorporate population dynamics (Sabelis et al. 1991). Most predator-prey models and food web models are deterministic and do not allow extinction from demographic stochasticity. In these models, either the interaction is deterministically unstable or the populations never go extinct (e.g., Crowley 1981; Sabelis et al. 1991). They tend to yield no difference in extinction proneness between fragmented and unfragmented populations, except in the cases where within-patch dynamics are unstable and where they generally favor metapopulations over single populations. If stochastic effects, or scaling, are important (which we would expect when the subject is extinction) models must deal with absolute numbers and not densities. Stochastic predator-prey models (e.g., Renshaw

1991) must solve the problem of how encounter rates scale with the spatial scale of a habitat remnant if they are to say something about the effects of habitat fragmentation on extinction risk. If encounter rates are scaled spatially in a neutral fashion, simple deterministic models (e.g., the Rosenzweig-MacArthur model) do not exhibit any effect of fragmentation (Burkey 1995a).

It is well known that a collection of unstable local populations may persist when linked by dispersal (Huffaker 1958; Levins 1969; Crowley 1981; de Roos et al. 1991 and references therein; Hanski 1991). Holyoak and Lawler (1996) recently demonstrated that a metapopulation of *Didinium* feeding on *Colpidium* could persist longer than a single population in a comparable volume. This does, however, require dispersal rates within a relatively narrow domain (Holyoak and Lawler 1996; Warren 1996 and references therein). Warren (1996) manipulated dispersal rates between patches in small and large metacommunities of 13 protist species. He found that higher dispersal rates had a slight effect on community and metacommunity species richness, "with a tendency for higher dispersal to slightly offset the rate of species loss" (p. 132). He found that a set of small patches with high and medium dispersal rates contained more species than a single large patch after 6 wk but not after 12 wk. Like most metapopulation models, these experiments differ from the ones I will describe here in that the authors deliberately used unstable systems while I use systems that are relatively persistent in large stock cultures. I chose initially persistent systems because I thought this the situation most relevant to conservation efforts—systems in which the species somehow coexist in an original habitat matrix and for which we are interested in what is likely to happen if humans alter that habitat matrix.

I assembled simple communities with three trophic levels of bacteria and protozoa and studied the persistence of the top predator under different regimes of habitat fragmentation. These model ecosystems typically consisted of four species of bacteria, a ciliate bacterivore, and a protozoan top predator that eats the bacterivore. Observing the presence or absence of the top predator over time I quantified its probability of extinction as a function of time in habitat patches of different sizes and in habitat areas of equal area fragmented into different number of subpopulations (i.e., subdivided into equal-sized patches that together are as large as the unfragmented treatment and as large as the total size of other fragmented treatments). I will refer to the reduction of habitat area available as "habitat loss" and to the subdivision of a given area into several smaller patches, without any loss of overall area, as "habitat fragmentation." In one community configuration, I connect the patches in fragmented systems with dispersal "corridors" to see if fragmentation has the same effect if the patches are not completely isolated from each other and to see if such corridors help to reduce the risk of extinction in fragmented systems.

Edge effects are an inherent aspect of habitat fragmentation since fragmentation increases the edge-to-area ratio. Several edge effects have been documented (see, e.g., Janzen 1983; Wilcove 1985; Lovejoy et al. 1986; Noss 1988; Burkey 1993a). Many edge effects are obvious and well understood. They may also obscure or confound other effects of fragmentation. This has been a problem in

studies that have claimed an increase in species richness with increased habitat fragmentation (e.g., Quinn and Harrison 1988). In these studies, one ends up counting many edge species that do not need conservation efforts and that do well in fragmented communities at the expense of threatened and endangered species. In a three-dimensional universe, such as the vessels in which I have studied protozoan communities, one can effectively separate the effects of increasing the amount of edge from other fragmentation effects by manipulating the depth relative to the diameter of experimental vessels.

MATERIAL AND METHODS

Study Organisms

At the base of each food chain were four species of bacteria: *Serratia marcescens, Bacillus subtilis, Bacillus cereus,* and *Proteus vulgaris.* The second link in the food chain was a single species of ciliate or flagellate that eats the bacteria, one of the following: *Colpidium striatum, Tetrahymena thermophila, Chilomonas paramecium, Bodo* sp., or an unidentified nanoflagellate. The top predator in each experiment was a large ciliate, either *Euplotes aediculatus* or *Didinium nasutum.* Both species will ingest bacteria as well as protist prey. *Euplotes* has a generation time of approximately 3–12 h depending on the temperature; for *Didinium* it is 3–6 h.

All the species I used are pelagic and do not utilize particular substrates such as edges or vessel bottoms especially. *Euplotes* has cirri on the ventral side, which they can use for walking on the bottom while feeding, but in my shallow cultures they utilize the entire water column. Cultures were shallow (3 mm), and the amount of bottom area (and surface area) were identical between treatments.

Experiments

Laboratory protocol.—Stock cultures of each community were maintained in approximately 100 mL of medium in 8-oz (240-mL) glass Qorpak jars with loose lids. (See Lawler and Morin 1993 for more information on the maintenance and dynamics of such cultures.) The experiments were conducted on species assemblages that persist for 2 mo or more in the stock cultures.

At the beginning of an experiment, protists and bacteria were introduced from the stock cultures, mixed in a large beaker, and distributed into experimental vessels of different sizes. Thus, all experimental vessels, regardless of size, were supplied with the same medium and the same concentrations of protists and bacteria. Nutrients were added every week, in the form of medium that was five times as concentrated as the standard medium, in the amount of 5% of vessel volume. This compensated for evaporation and maintained nutrient concentrations.

Experimental design.—I observed the presence or absence of predator in each vessel over time and compared the persistence of predators in vessels of different sizes and in volumes subjected to different degrees of fragmentation. Un-

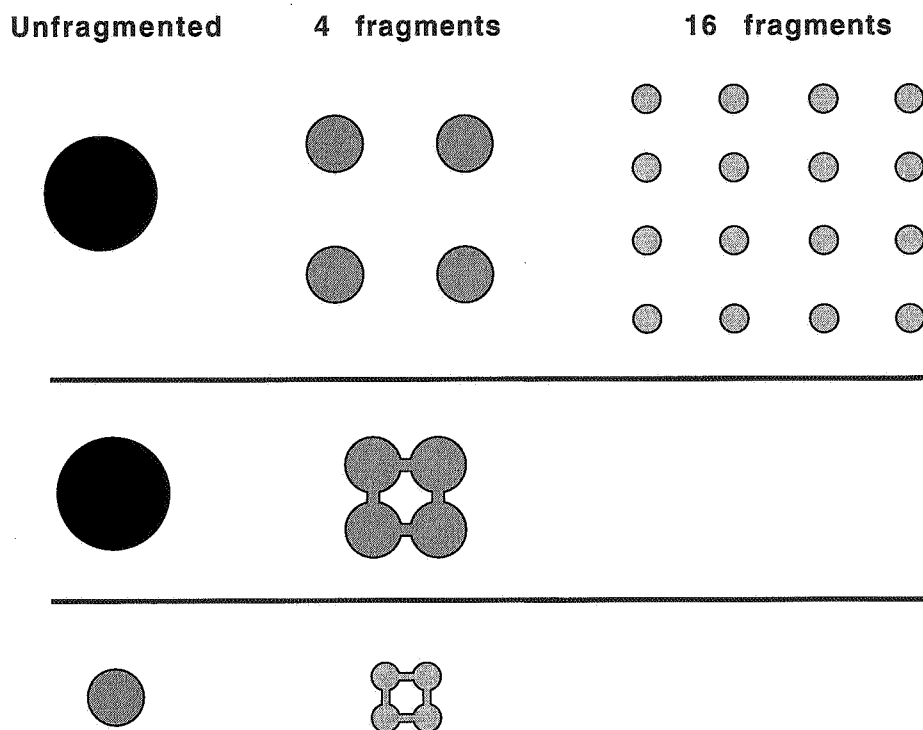# Unfragmented   4 fragments   16 fragments

FIG. 1.—Experimental design. In most experiments, the persistence time of a single large population (6.4 mL) was compared with a set of four populations (1.6 mL each) and 16 populations (0.4 mL) each. One experiment compared the persistence time of a single XL population to that of a set of four L populations linked with dispersal corridors. One similar experiment, with identical initial conditions, compared a single L population with a set of four linked M populations. Not explicitly shown are the simultaneous three-way comparisons in one community configuration, between unfragmented populations, fragmented systems without corridors, and fragmented systems with corridors between subpopulations.

fragmented populations (single large vessel) were compared with fragmented populations (sets of smaller vessels with the same total size as the single large vessel), and less fragmented populations with more fragmented populations (e.g., 16 small vessels with four intermediate-sized vessels or 16 intermediate vessels with four large vessels). Figure 1 illustrates the comparisons made. In one set of experiments, the fragmented populations were linked by dispersal corridors. The experimental vessels were pits of different sizes in Plexiglas plates, scaled so that total bottom and surface areas were identical across treatments. Corridors linking patches in a metapopulation structure were created by removing part of the cylinder wall separating adjacent sets of four vessels. All species dispersed easily through the corridors. I compared the extinction times of the unfragmented populations with that of the fragmented systems and metapopulations, and the persistence of the fragmented systems with or without corridors between subpopulations.

I also observed the presence and absence of the prey species. However, either the prey species never went extinct in any vessel of any size or all prey populations went extinct between the start of the experiment and the next observation date. Consequently, there was no basis for an analysis of extinction times for the prey. All species were present in substantial numbers in all vessels at the start of the experiment.

The different fragment sizes were small (S) vessels, holding 0.1-mL culture, medium (M) vessels with 0.4-mL culture, large (L) with 1.6-mL culture, and extra large (XL) with 6.4-mL culture. Vessels holding smaller volumes of medium (and consequently smaller populations) were smaller in diameter, so that the surface and bottom areas of smaller vessels were exactly one-fourth that of the next larger size class. Consequently there were four S vessels (holding 0.1 mL each) to each M vessel (holding 0.4 mL), four M vessels to each L vessel, and so on. Across all treatments of different degrees of fragmentation, the overall volume, surface and bottom areas, and initial conditions were identical and hence population sizes were expected to be similar across all treatments. An XL vessel was 5 cm in diameter, an L vessel 2.5 cm, and so on. Since the depth of each volume was small (3 mm) compared with the bottom and surface area, the total amount of "edge" (surface, bottom, and sides) changed only slightly between treatments of different degrees of fragmentation. In two-dimensional systems, the edge-to-area ratios change much more with fragmentation than in these shallow three dimensional systems. Some measure of scale can be gained by the estimate that an unstarved *Didinium* may swim 0.5 mm/s (but they turn at a rate of 55°/ s; M. Holyoak and N. Kapadia unpublished data). Holyoak and Lawler (1996) observed that some individuals managed to disperse between vessels 11.2 cm apart within 1 h.

All vessels were inspected directly under a binocular lens (6×–50× magnification) for presence or absence of the focal species. In most experiments, the vessels were inspected weekly (table 1). Populations were observed for at least 2 mo, or until the top predator was extinct in all treatments.

All vessels were placed on test tube holders in a water bath with a clear Plexiglas cover at ambient temperature. Evaporation in experimental vessels was minimal due to the saturated air above the water bath and was equivalent across treatments due to the identical surface areas of all treatments. All vessels were covered by loosely fitting lids. Experimental units were not mechanically mixed.

For a summary of the experiments, the species assemblages utilized, abbreviated codes for the protist species in the experiment, and the schedule for observing the abundance of protozoa populations, see table 1.

Initial population size.—In three experiments (see table 1), initial population sizes of the predators were estimated in medium-sized vessels by counting all the top predators in the vessel under the binocular lens. Each M vessel was placed under the dissecting scope, and each individual predator was counted directly, without sampling. Initial predator densities were later correlated with the time to extinction to look for an effect of initial population size within vessels of a given size.

TABLE 1

COMMUNITY CONFIGURATIONS AND CONDITIONS FOR EXPERIMENTS

CODE	BACTERIVORE	PREDATOR	REPLICATES AT EACH SPATIAL SCALE				OBSERVATION SCHEDULE	
			S (.1 mL)	M (.4 mL)	L (1.6 mL)	XL (6.4 mL)	Check	Count
Tet-Did	Tetrahymena	Didinium	...	150	96	34	Weekly	...
Bodo-Eup	Bodo	Euplotes	288	150	96	34	Weekly*	...
Nano-Eup	Anonymous nanoflagellate	Euplotes	...	150	96	34	Weekly	$t = 0$†
Col-Eup 1	Colpidium	Euplotes	...	...	20	5	...	Every 2d day
Col-Eup 2	Colpidium	Euplotes	...	100	...	...	Every 2d day	$t = 0$†
Col-Eup 3	Colpidium	Euplotes	...	50	72	30	Weekly	...
Chilo-Eup	Chilomonas	Euplotes	...	138	116	24	Every 4th day	$t = 0$†

NOTE.—Sample sizes for fragmented systems are obtained by integer division of the number of replicates of the appropriate vessel size (see also the other tables). See table 5 for experiments involving fragmented systems with dispersal corridors between patches.
* Slightly variable observation schedule; see figure 2.
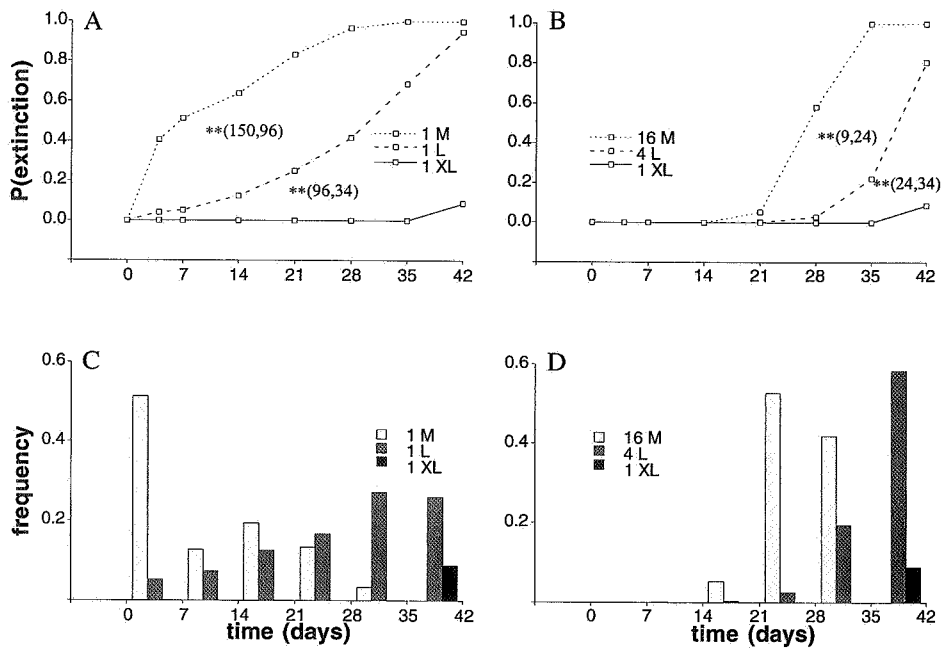† Counts of initial population sizes in medium-sized vessels only.

FIG. 2.—Persistence times of *Didinium nasutum* when fed on *Tetrahymena thermophila*. A, Extinction probabilities in patches of different sizes. B, Extinction probabilities over time in systems of different degrees of fragmentation. C, The distributions of extinction times for single populations of different sizes. D, Distributions of extinction times for entire systems with different degrees of fragmentation. Small populations go extinct sooner than large populations. **(n_1, n_2) indicates that the treatment above and below are significantly different at $P < .0001$ (based on normal approximations to the Mann-Whitney U-test on times to extinction, corrected for ties); n_1 and n_2 are sample sizes for the treatment above and below where they are located in the figures, respectively.

RESULTS

In all experiments, populations went extinct faster in small vessels than in large vessels. Fragmented systems went extinct faster than unfragmented systems of the same total size. In all pairwise comparisons of a more fragmented system with a less fragmented system, except one, the less fragmented populations persisted significantly longer than the more fragmented system. In the one exception, in Chilo-Eup the *Euplotes* populations in one large fragment went extinct sooner than in the sets of four medium-sized fragments. This was an unusual system in that the prey species were overexploited and went extinct before the first sampling date (leaving *Euplotes* to feed on bacteria).

Didinium *on* Tetrahymena

The persistence of *Didinium* is shown in figure 2. Populations in small isolated vessels went extinct much sooner than populations in larger vessels (1 XL vs. 1 L: $Z = -8.13$; 1 L vs. 1 M: $Z = -10.11$; 1 XL vs. 1 M: $Z = -9.32$;

TABLE 2

Results of Paired Comparisons of the Top Predator *Didinium*,
Feeding on *Tetrahymena* (tet-did)

Treatment 1	Treatment 2	Tied Z	Tied P	n_1	n_2	Mean Rank 1	Mean Rank 2	Number of Ties
1 XL	1 L	−8.13	<.0001	34	96	109.68	49.85	7
1 L	1 M	−10.11	<.0001	96	150	179.93	87.38	8
1 XL	1 M	−9.32	<.0001	34	150	167.50	75.50	8
1 XL	4 L	−5.67	<.0001	34	24	38.62	16.58	3
1 L	4 M	−4.13	<.0001	96	37	75.40	45.22	8
1 XL	16 M	−5.79	<.0001	34	9	26.5	5.00	4

Note.—Tied Z values are normal approximations to the Mann-Whitney U-test corrected for ties; tied P values are the significance levels of the tied Z statistic. Sample sizes n_1 and n_2 are for treatments 1 and 2, respectively. Low rank values indicate early extinction times. Because P values of all pairwise comparisons are very low, no correction has been made for multiple comparisons.
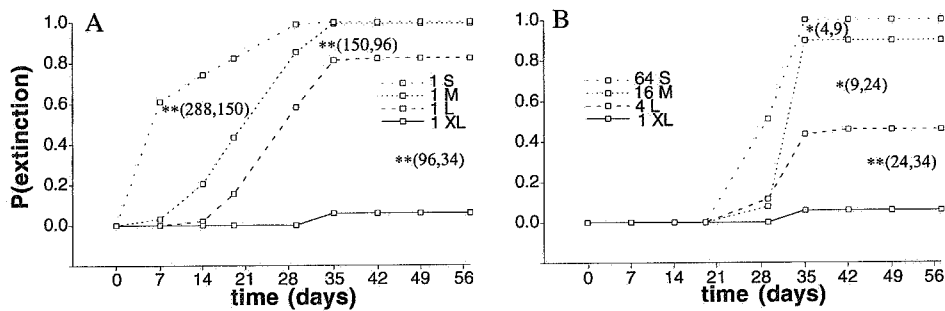

Fig. 3.—Persistence times for *Euplotes aediculatus* when fed on *Bodo* sp. *A*, Extinction probabilities in patches of different sizes. *B*, Extinction probabilities over time in systems of different degrees of fragmentation. * = significant at $P < .025$ in a Mann-Whitney U-test corrected for ties. **(n_1, n_2) as in figure 2.

$P < .0001$ for all). This effect was so strong that entire fragmented systems always went extinct sooner than comparable less fragmented systems (1 XL vs. 4 L: $Z = -5.67$; 1 L vs. 4 M: $Z = -4.13$; 1 XL vs. 16 M: $Z = -5.79$; 4 L vs. 16 M: $Z = -4.23$; $P < .0001$ for all; see table 2).

Euplotes *on* Bodo

The persistence of *Euplotes* in Bodo-Eup is shown in figure 3. Extinction times were always shorter in small vessels than in large vessels and in more fragmented systems than in less fragmented systems (table 3).

Euplotes *on Anonymous Nanoflagellate*

In Nano-Eup, *Euplotes* went extinct faster in small vessels than in large vessels and faster in fragmented systems than in unfragmented systems (fig. 4, table 4).

TABLE 3

RESULTS OF PAIRED COMPARISONS OF RANKED PERSISTENCE TIMES OF THE TOP
PREDATOR, *EUPLOTES*, FEEDING ON *BODO* (BODO-EUP)

Treatment 1	Treatment 2	Tied Z	Tied P	n_1	n_2	Mean Rank 1	Mean Rank 2	Number of Ties
1 XL	1 L	−7.48	<.0001	34	96	104.79	51.58	5
1 L	1 M	−6.07	<.0001	96	150	156.35	102.47	6
1 M	1 S	−11.96	<.0001	150	288	315.00	169.76	5
1 XL	4 L	−4.23	<.0001	34	24	36.06	20.21	3
1 L*	4 M	−1.45	.073	96	37	69.84	59.63	5
1 M	4 S	−5.09	<.0001	150	72	126.15	80.97	5
1 XL	16 M	−4.78	<.0001	34	9	25.91	7.22	3
1 XL	64 S	−4.12	<.0001	34	4	21.47	2.75	3
1 L	16 S	−3.61	.0001	96	18	62.11	32.92	5
4 L	16 M	−1.94	.025	24	9	18.90	11.94	3
4 M	16 S	−2.66	.004	37	18	31.73	20.33	4
4 L	64 S	−2.39	.008	24	4	15.94	5.88	3
16 M	64 S	−2.15	.016	9	4	8.33	4.00	2

*Not significant ($.1 < P < .05$) in Mann-Whitney U-test, but significant ($P < .01$) in a two-tailed unpaired t-test (which utilizes information about the absolute magnitude of observations).
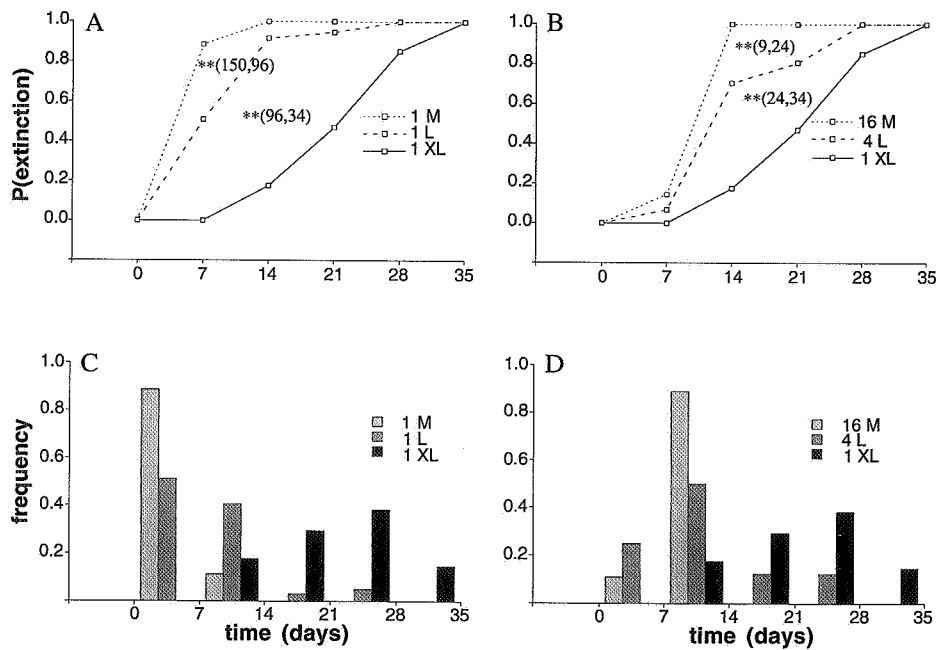

FIG. 4.—Persistence of *Euplotes aediculatus* populations over time in a community when fed on an anonymous nanoflagellate. See figure 2 for **(n_1, n_2) and for *A–D* designations.

TABLE 4

RESULTS OF PAIRED COMPARISONS OF RANKED PERSISTENCE TIMES OF TOP PREDATORS FOR
EUPLOTES ON AN ANONYMOUS NANOFLAGELLATE AND FOR *EUPLOTES* ON *COLPIDIUM*

Code/ Treatment 1	Treatment 2	Tied Z	Tied P	n_1	n_2	Mean Rank 1	Mean Rank 2	Number of Ties
Nano-Eup:								
1 XL	1 L	−7.64	<.0001	34	96	105.78	51.23	5
1 L	1 M	−6.68	<.0001	96	150	152.43	104.99	4
1 XL	1 M	−11.32	<.0001	34	150	166.00	75.84	5
1 XL	4 L	−4.43	<.0001	34	24	37.49	18.19	5
1 L	4 M	−1.70	.045	96	37	70.10	58.96	4
1 XL	16 M	−4.01	<.0001	34	9	25.79	7.67	4
Col-Eup 3:								
1 XL	1 L	−6.57	<.0001	30	72	77.72	40.58	5
1 L	1 M	−4.04	<.0001	72	50	70.92	47.94	3
1 XL	1 M	−6.81	<.0001	30	50	62.20	27.48	6
1 XL	4 L	−3.95	<.0001	30	19	30.58	16.18	4
1 L*	4 M	−1.45	.073	72	12	43.79	34.75	2
1 XL	16 M	−2.53	.006	30	4	18.95	6.63	4

* Nonsignificant result in a very weak test.

Euplotes *on* Colpidium

In all three experiments with *Colpidium* and *Euplotes,* the prey were overexploited and went extinct in all vessels, regardless of size, within 2–4 d. In comparison, both species coexisted for the duration of the experiment in four 100-mL stock cultures, indicating a possible threshold effect of reducing area. After the disappearance of *Colpidium,* I expected rapid decline and extinction of *Euplotes. Euplotes* did decline to extinction, but over a time period that indicates they could survive on bacteria. Given the steady decline, one would expect the difference between treatments to be slight or absent. Yet in Col-Eup 1, all fragmented systems went extinct before their unfragmented paired system. This is the most extreme possible outcome, and its probability under the null hypothesis is $P = .031$ (sign test). In Col-Eup 3, *Euplotes* went extinct sooner in small vessels than in larger vessels and sooner in fragmented systems than in unfragmented systems (table 4).

Euplotes *on* Chilomonas

Euplotes quickly overexploited their prey in all vessels of all treatments, driving *Chilomonas* extinct within 4 d. Subsequently, *Euplotes* were sustained on bacteria. *Euplotes* went extinct sooner in small vessels than in larger vessels. This difference was highly significant in all comparisons (table 5). A set of four extra large populations (4 XL) persisted longer than a set of 16 large populations (16 L), but a single large population (L) went extinct sooner than a set of four medium populations (4 M; see table 5). In the latter comparison, the two samples, while statistically different, are biologically similar. The difference in mean rank is slight, given the large sample sizes (table 5), and the median persistence times (56 and 60 d, respectively) are different from each other only by one time

TABLE 5

PAIRED COMPARISONS OF THE RANKED PERSISTENCE TIMES OF THE TOP PREDATOR,
EUPLOTES, FEEDING ON *CHILOMONAS* (CHILO-EUP)

Treatment 1	Treatment 2	Tied Z	Tied P	n_1	n_2	Mean Rank 1	Mean Rank 2	Number of Ties
1 XL	1 L	−4.22	<.0001	24	116	102.23	63.94	15
1 L	1 M	−3.68	<.0001	116	138	145.93	112.01	17
1 XL	1 M	−5.55	<.0001	24	138	130.23	73.03	15
1 XL*	4 L	−1.36	.088	24	29	30.15	24.40	11
1 L†	4 M	−2.87	.002	116	34	70.01	94.24	16
1 XL*	16 M	−.175	.430	24	8	16.33	17.00	6
4 XL	16 L	−2.91	.002	6	7	10.33	4.14	2
1 XL	4 L (linked)	−4.41	<.0001	24	16	27.15	10.53	11
1 L	4 M (linked)	−3.10	.001	116	18	71.57	41.25	15
4 L	4 L (linked)	−4.46	<.0001	29	16	29.45	11.31	13
4 M	4 M (linked)	−4.23	<.0001	25	18	28.84	12.50	12

* Nonsignificant result in a very weak test.
† Single pairwise comparison, where most fragmented treatment has the longest extinction time.

step in the observation schedule. Persistence time ranges were 24–85 d and 28–85 d, respectively. The differences between 1 XL and 4 L, and between 1 XL and 16 M, were not significantly different from zero in Mann-Whitney U-tests. (This nonparametric test is particularly weak in cases where one treatment has a few early occurrences but many late occurrences.)

Effects of Dispersal Corridors

In both experiments where the viability of metapopulations (sets of small populations linked by dispersal corridors) were compared with that of unfragmented populations with the same amount of available habitat, the metapopulations always went extinct sooner (fig. 5, table 5). Metapopulations of four M-sized subpopulations linked by dispersal corridors went extinct sooner than single L (unfragmented) populations, and metapopulations of four L populations went extinct before single XL populations. This difference was highly significant in both experiments ($Z = -3.10$, $P = .001$ and $Z = -4.41$, $P < .0001$, respectively; see also fig. 5).

Perhaps surprisingly, the metapopulations went extinct sooner than equally fragmented systems that were not linked by dispersal corridors (fig. 6, table 5). A set of four completely isolated M-sized populations persisted longer than a metapopulation of four M-sized populations linked together ($Z = -4.29$, $P < .0001$), and a set of four isolated L populations persisted longer than a metapopulation of four L populations ($Z = -4.46$, $P < .0001$).

Initial Population Sizes

No effect of initial population size on time to extinction was detected within vessel sizes (M vessels; $r = 0.339$, $n = 30$, $P = .07$ in Nano-Eup; $r = 0.041$, $n = 100$, $P = .68$ in Col-Eup 2; $r = -0.08$, $n = 100$, $P > .5$ in Chilo-Eup). Initial population size ranges were four to 19, five to 28, and 22–91 individuals,
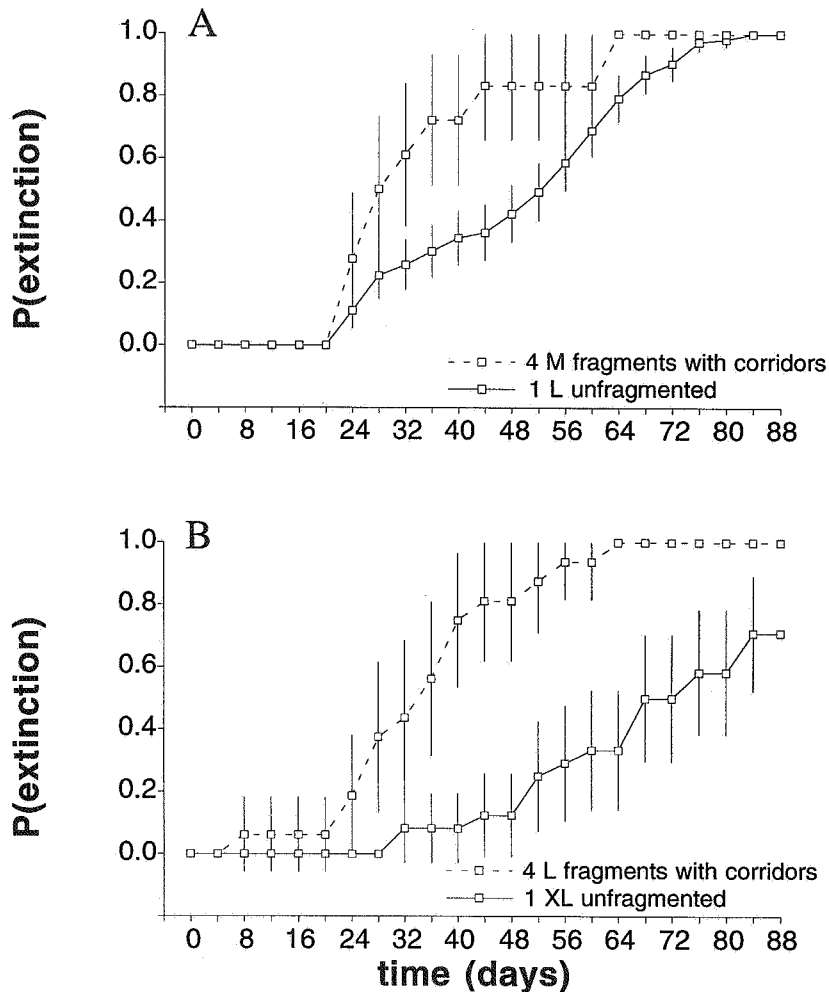
FIG. 5.—The probability of extinction as a function of time, comparing unfragmented systems with fragmented systems where subpopulations are linked by dispersal corridors (metapopulations). A, One large unfragmented population compared with a metapopulation of four medium-sized fragments. B, One extra large unfragmented population compared with a metapopulation of four large fragments. Error bars are ±2 SE (approximate confidence intervals). Error bars are larger in this experiment than the others because the number of replicates are substantially smaller.

respectively. Extinction time ranges were 7–14 d, 16 to >60 d, and 22 to >88 d, respectively.

Distribution of Extinction Times

In none of the treatments was the geometric distribution a good approximation of the distribution of extinction times (figs. 2C, D; 4C, D; 7). There were
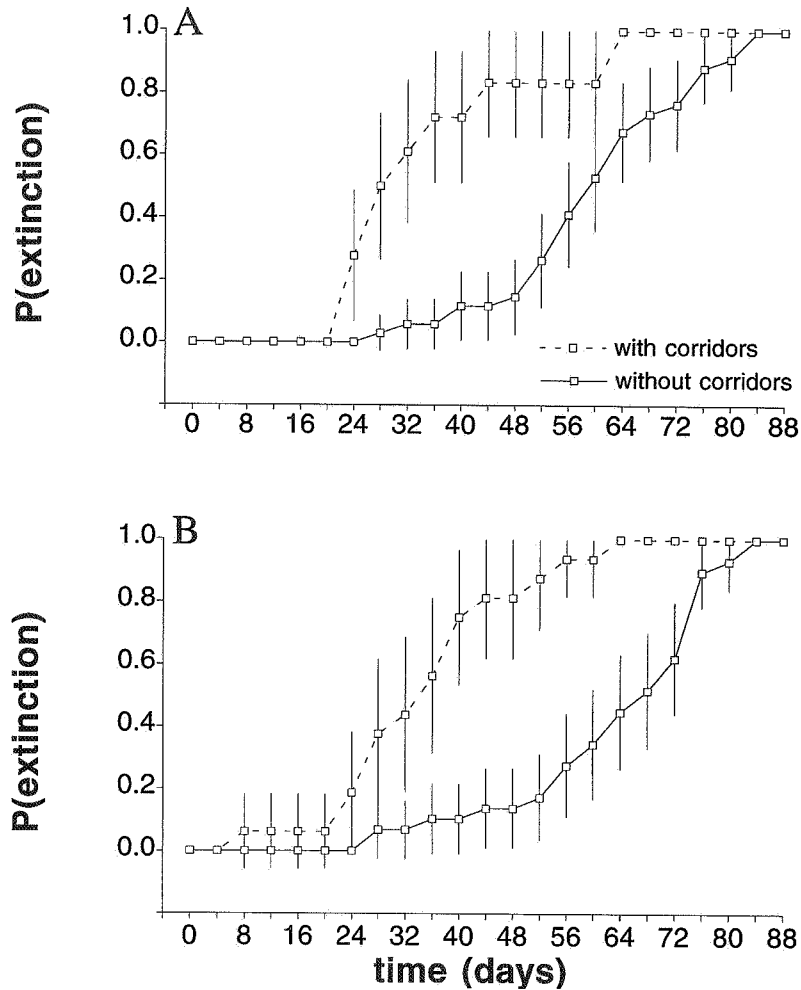
FIG. 6.—The probability of extinction as a function of time, comparing fragmented systems witout dispersal between patches to fragmented systems where subpopulations are linked by dispersal corridors (metapopulations). A, Four medium fragments. B, Four large fragments.

too few extinctions in the short term. The distributions tended to have long right-hand tails. Various forms of the gamma distribution approximate the different sample distributions better (see also Burkey 1995a). In M and L vessels of Chilo-Eup, the distribution of extinction times were bimodal (or had more than two modes)—which does not fit any standard statistical distribution (fig. 7).

DISCUSSION

In every experiment, populations of the top predators went extinct sooner in small vessels than in larger vessels. This effect was so strong that sets of small
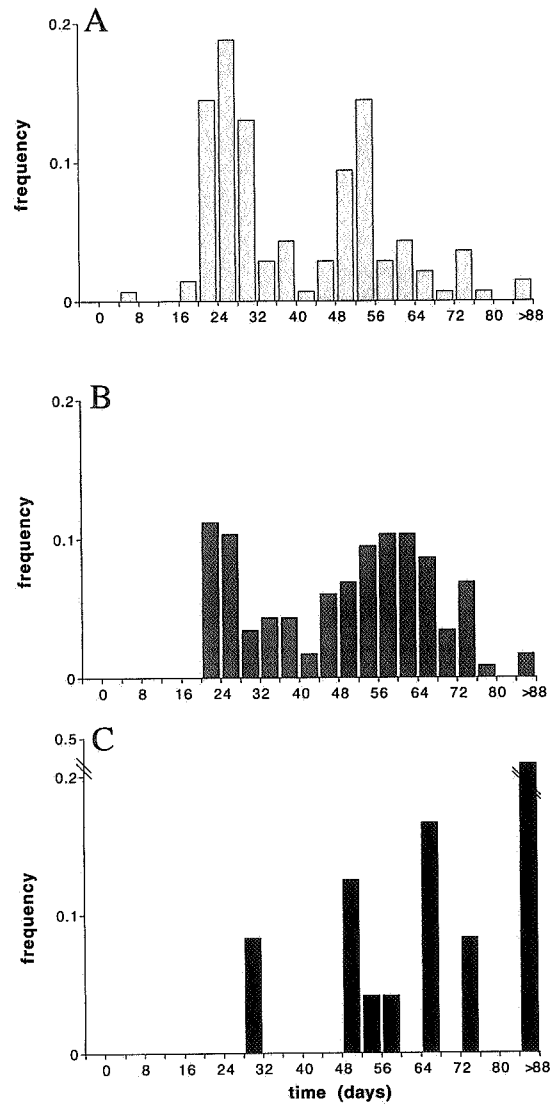
FIG. 7.—The distribution of extinction times for single populations of *Euplotes* in Chilo-Eup. Nearly 50% of the extra large populations were still extant when the experiment was terminated after 88 d (note the broken Y-axis for the last bar in C). A, One medium; B, one large; C, one extra large.

populations went extinct significantly sooner than continuous large populations even when they had the same amount of total available habitat. In fragmented systems, the top predators went extinct more quickly than in less fragmented systems. In every pairwise comparison in every experiment, except one, the more highly fragmented system had shorter median and mean times to extinction than the less fragmented system. In the one exception—a single large popu-

lation of *Euplotes aediculatus* on *Chilomonas paramecium* had persistence times shorter than a set of four medium populations—the predator had driven the prey species extinct almost immediately by overexploitation and persisted solely on the bacteria (and the difference in persistence times was very slight). Overall, these experimental systems—which presumably experience both demographic and environmental stochasticity, population genetic processes, and "catastrophes" just like "natural" populations—persist longer when they are continuous than when they are fragmented into several smaller subpopulations. As biological models, they give an indication of how anthropogenic habitat fragmentation may affect the viability of species in previously continuous landscapes.

Robustness

Every experimental community investigated in this study showed the same result: the top predator went extinct sooner in a fragmented system than in a continuous system. This is true at all spatial scales investigated and across a variety of initial conditions and timescales. The same results were obtained in two pilot studies using different nutrient concentrations and vessels ranging from 0.1 mL to 96 mL in size. In Col-Eup 1–3 and Chilo-Eup, the prey species went rapidly extinct, and the rapid loss of the predator seemed assured, regardless of the degree of fragmentation. Yet the treatment effect was generally maintained, and most unfragmented populations persisted a long time past the extinction of their fragmented counterparts.

Except under some unusual circumstances, individual-based simulations of predator-prey models with demographic stochasticity (and highly nonlinear scaling of encounter rates) yield results consistent with the results of the present experiments (Burkey 1995a). Large patches yield persistence times so much longer than small patches that the redundancy in fragmented systems is insufficient to yield a longer maximum extinction time from the set of smaller patches. The one exception to the general rule, observed in Chilo-Eup, may be because of gradual, deterministic decay of the system caused by the top predators inefficiency on bacterial prey. If, for instance, equilibrium population size (carrying capacity) decays with time in all patches, the advantage to large systems may be reduced so much that the added redundancy in fragmented systems could overcompensate for the smaller size of their patches. Again, this is easier in systems where the distribution of extinction times have relatively long right tales.

The present results corroborate the results obtained by Forney and Gilpin (1989) on the effects of habit fragmentation on extinction risk, in single species lab populations of *Drosophila pseudoobscura*. Theirs was a single species community where population numbers were so low that the effects were likely due entirely to demographic stochasticity. The results are also consistent with simulation results obtained in earlier studies (Burkey 1989, 1995a) and the mechanism proposed therein, as well as results from a model calibrated with estimated extinction rates in oceanic and terrestrial "archipelagoes" (Burkey 1995b).

Habitat patches in the "real world" may certainly experience greater spatiotemporal variation between them in weather and other environmental perturbations, and thus fragmented systems may benefit relatively more from the sort of

spatial bet-hedging that some spatial segregation affords than they do in these experimental systems. On the other hand, real habitat patches or subcomponents in a reserve system may also be relatively close together and thus have a relatively high degree of correlation—especially if they are to represent the same habitat type and play a role in the management of a particular focal species. Computer simulations indicate that the spatial independence and the severity of such perturbations must be quite substantial before the benefits of spatial bet-hedging can outweigh the benefits of reduced susceptibility to demographic stochasticity in a large continuous patch (Burkey 1995a). Of course, conditions need not be uniform within a large continuous patch either.

In other microcosm food webs, Spencer and Warren (M. Spencer and P. H. Warren, unpublished manuscript) found that some species' relative abundance were affected by habitat size but without any consistent pattern of responses (see also Warren 1996). Spencer and Warren (1996) found that larger microcosms supported food webs with more species and longer foodchains. Luckinbill (1974) found that Didinium nasutum and their prey, Paramecium aurelia, coexisted longer (82 h) in a large experimental volume (1,000 mL) than in smaller vessels, where Didinium captured all the Paramecium in 2.8–21 h (0.1–100 mL volumes). A large volume and food limitations on the prey were necessary conditions for a persistent interaction. Elsewhere, Luckinbill (1973) showed that the system could persist when methyl cellulose was added to the medium, slowing the movements of both organisms. Increasing volumes and decreasing movement rates seems to be another way to provide refuge for the prey (Gause et al. 1936).

Causes of Extinction

The protozoa and bacteria in these experiments experience a diversity of biological processes and interactions among them: demographic and environmental stochasticity, various population genetic processes, different forms of density dependence, and so forth. Demographic stochasticity with density dependence in the demographic rates causes extinction rates to be higher in fragmented systems in the way seen here (Burkey 1989, 1995a) and is at least a partial explanation. Environmental stochasticity and catastrophes tend to reduce the relative effect of fragmentation if the spatial covariance is large (Burkey 1995a) and to bias in favor of added redundancy to the extent that they are spatially uncorrelated between subpopulations (Goodman 1987; Burkey 1995a). While environmental stochasticity and catastrophes, if sufficiently severe and at least partially uncorrelated across patches, may conceivably overwhelm the effect of demographic stochasticity and other factors that favor continuous populations over fragmented populations, that did not happen in these systems.

The bimodal distribution of extinction times in Chilo-Eup suggest a predator-prey oscillation in which the predators tend to go extinct when they are at low population sizes in the troughs of the oscillation; this is consistent with demographic stochasticity as a proximate causal mechanism. In all vessels, the initial predator population sizes were substantially above the level where they risked being absent, and in some experiments their population sizes attained magni-

tudes greater than 2,000 individuals in an XL vessel (e.g., in Bodo-Eup). Several authors (e.g., MacArthur and Wilson 1967; Shaffer and Samson 1985) have concluded, on the basis of simple models, that demographic stochasticity poses an insignificant threat to population viability above a moderate range of carrying capacities and population sizes (e.g., >50 individuals). However, their single species models do not allow for any mechanism whereby population sizes are likely to be brought down occasionally to levels much below carrying capacity. Predator-prey oscillations and disturbances of various kinds have the potential to bring population sizes down periodically to low levels where they go extinct for stochastic reasons, and such factors must be taken into consideration in population viability analyses.

The biomodal distribution of extinction times in Chilo-Eup may also be related to an initial instability in the predator-prey interaction. There were no attempts in these experiments to allow the systems to enter a stationary state following their isolation in experimental vessels (which are much smaller than the stock cultures). The situation is analogous to what one might expect following an anthropogenic disturbance where populations become confined in a smaller subsection of a previously continuous habitat area, either in several patches or in a single patch. Such a disturbance may destabilize the system initially, especially as one might expect an unusually high initial density of motile organisms following immigration from the areas that have been altered. It may be that many experimental populations first went extinct because of an initial instability and that populations that made it through this transient period persisted for awhile before succumbing to other factors, such as demographic stochasticity. It may be that the first bout of extinctions were populations that were unsuccessful in making the transition to feeding on bacteria following the extinction of *Chilomonas* and that the rest went extinct later for other reasons, including factors peculiar to interactions with the new bacterial prey or stochastic fluctuations around a new equilibrium.

Distribution of Extinction Times

The distributions of extinction times in these experiments did not approximate the geometric distribution in any treatment. Various shapes of the gamma distribution fit the experimental data better, for either single populations or sets of populations (see figs. 2, 3, 4; see also Burkey 1995a). This is to be expected, as few populations go extinct immediately. Indeed, in the analysis of stochastic birth-death processes, the time interval is usually defined so short that the probability of two or more events in a time interval is negligible, and the earliest the population can go extinct is after a number of time intervals approximately equal to the initial population size. If the focal species is present initially in at least moderate numbers, there are more different paths to extinction in a chain of birth and death events on intermediate timescales than on very short timescales. The gamma distribution was predicted by my analyses of stochastic birth-death models with density dependence in demographic rates—and similar results obtained in a stochastic predator-prey simulation model (Burkey 1995a). Previous studies reported approximately geometric distributions because the re-

sults were displayed in histogram form, where the few early extinctions were pooled with a large number of intermediate extinction times.

Predictors of Extinction Proneness

No effect of initial population size on persistence time was detected within medium-sized vessels. The effect of vessel ("fragment") size was great in all experiments, and the vessel size is of course directly correlated with initial population size since all populations were initiated from the same stock culture. The area effect and the initial population size effect (if there is one) are of course confounded. The lack of any effect of initial population size is to be expected if populations tend toward a carrying capacity determined by the amount of available habitat. A population that starts out small may certainly go to extinction rapidly, but they have great growth potential and may just as well undergo extensive fluctuations before eventually going extinct. The available habitat area is expected to limit the range over which the population size will fluctuate over time and thus have a more lasting impact on the persistence of the species than the initial population size. The lack of dependence between initial population size and time to extinction corroborates findings from several theoretical models. Richter-Dyn and Goel (1972) and Leigh (1981) showed that the mean time to extinction is nearly independent of initial population size under demographic or environmental stochasticity (for populations with positive long-term growth rates and sufficiently large initial size). Lande (1993) obtained a similar result for populations subject to random catastrophes.

The range and variation of population fluctuations is smaller for a set of small populations than for a single large population since the subpopulations can be partially out of phase. This does not, however, translate into higher persistence across treatments in the present experiments. In otherwise identical populations, one would expect population variability to be a powerful predictor of extinction proneness (Wright and Hubbell 1983; Bengston and Milbrink 1995), but it appears that other factors overcompensate for any advantage resulting from reduced metapopulation variability in fragmented systems. Lower average population sizes and correspondingly shorter persistence times may result from reduced expected overall population growth rates in a set of small populations because of the variance in population densities between subpopulations and the fact that phase diagrams for populations with negative density dependence tend to be concave down (see Burkey 1995a).

Dispersal Corridors

In both of the two experiments where fragmented systems were linked by dispersal corridors, the unfragmented systems still persisted significantly longer than the fragmented systems. In fact, when the linked systems in these experiments are compared with their unlinked counterparts, the unlinked populations actually persisted longer than the linked populations. This is counter to the assumptions made by MacArthur and Wilson's (1967) "Theory of Island Biogeography," Brown and Kodric-Brown's (1977) "rescue effect," and the widely

held notion that if reserves are fragmented, the fragments should be close to-gether and linked by dispersal corridors to minimize the risk of extinction (Dia-mond 1975; Wilson and Willis 1975). Recall, however, that these results came from a configuration where the predator, *Euplotes aediculatus,* had driven the prey, *Chilomonas paramecium,* to almost immediate extinction through overex-ploitation and was persisting on bacteria. This configuration also had odd distri-butions of extinction times, and the single pairwise comparison where the effect of fragmentation went in the opposite direction from the others

The spread of disease is one reason why metapopulations may suffer greater extinction risk than sets of isolated patches (Hess 1994). Corridors also facilitate the spread of disease within a reserve system, reducing one of the expected ben-efits relative to unfragmented systems. Another potential explanation is edge ef-fects. I took special pains to limit differences in the amount of edge in the other treatments, but with the presence of the corridors there was necessarily a slight increase in the amount of edge relative to surface area or volume. Increased edge-to-area ratios are inherent to the fragmentation process in nature. *Euplotes* do tend to feed on the bottom of experimental vessels, but in this experiment the protist prey had gone extinct and *Euplotes* was feeding on bacteria with very short division times, so I doubt that increased feeding rates would cause an in-crease in extinction risk.

Unless this is simply an aberrant experiment, I would like to propose an alter-native mechanism to account for the effect of corridors. The stream of dispersers between patches act to synchronize the population dynamics between fragments, making them more similar in their extinction dynamics than random indepen-dent populations of the same size (see de Roos et al. 1991 and references therein; Allen et al. 1993). With a high degree of correlation between subpopu-lations, the extinction process for the metapopulation as a whole becomes like a random process where one draws once from one distribution (or, rather, four draws with very little spread), rather than four times independently from a distri-bution with a smaller mean. When the distribution of extinction times for a sin-gle population has a long right tail, drawing four times from the latter distribu-tion (with greater independence) yields a greater time to extinction than drawing once from the former (or drawing four times with very little spread). Dispersal between subpopulations does not make the metapopulation equivalent to a single panmictic population; individual subpopulations are still locally bounded by the physical limits of their patch in ways that arbitrary subcomponents of a large continuous patch are not. In short, fragmentation imposes more boundaries on populations, within which they must face local competition and local caps on population size. Instead, the distribution of extinction times for subpopulations in a metapopulation is somewhere in between the distribution for subpopulations in a fragmented system with completely isolated patches and that of a single large continuous patch. Since the variation in extinction times between subpopu-lations in a metapopulation is reduced relative to that in a set of completely iso-lated subpopulations, the distribution of extinction times for the entire system (i.e., the maximum extinction time for any subpopulation) may be greater in a

set of completely isolated patches, as well as in the comparable single large patch.

Corridors partially eliminate one of the perceived benefits of fragmented systems, namely, the independence of spatially separated habitat patches. Another reason why dispersal corridors may not do much to enhance the persistence of metapopulations is that the subpopulations may be highly correlated anyway. This could be due to similar initial conditions after fragmentation or to any important large-scale environmental variability. If all populations are at low densities at the same time, or go extinct at approximately the same time, there is no benefit to spreading of risk, and the rescue effect would be slight at best. The benefit of dispersal between subpopulations is further reduced because individuals will tend not to leave one patch for another, and if they do, any increase in viability to its adopted population comes at a cost to the viability of the population it is leaving. Holyoak and Lawler (1996) also found that predator-prey ratios were higher in subdivided microcosms with corridors than in undivided microcosms of the same total size. If this were true in my systems as well, it may have contributed to the early extinction of fragmented systems with corridors.

Some computer simulations (Burkey 1989, 1995a) and Forney and Gilpin's (1989) lab experiment on *Drosophila* support the claim that dispersal between habitat fragments can alleviate the threat of system-wide extinction. One should not conclude on the basis of this experiment alone that habitat corridors between patches in fragmented landscapes are useless or even detrimental to the viability of species. However, these results show the need for caution in uncritically viewing such corridors as cure-alls for the ills of fragmented populations. The establishment of wildlife corridors should not be used as an excuse for continuing to fragment natural habitats, and corridors may even be detrimental in some cases (see also Simberloff et al. 1992; Hess 1994).

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