

# Pattern Does Not Equal Process: What Does Patch Occupancy Really Tell Us about Metapopulation Dynamics?

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**ABSTRACT:** Patch occupancy surveys are commonly used to parameterize metapopulation models. If isolation predicts patch occupancy, this is generally attributed to a balance between distance-dependent recolonization and spatially independent extinctions. We investigated whether similar patterns could also be generated by a process of spatially correlated extinctions following a unique colonization event (analogous to nonequilibrium processes in island biogeography). We simulated effects of spatially correlated extinctions on patterns of patch occupancy among pikas (*Ochotona princeps*) at Bodie, California, using randomly located extinction disks to represent the likely effects of predation. Our simulations produced similar patterns to those cited as evidence of balanced metapopulation dynamics. Simulations using a variety of disk sizes and patch configurations confirmed that our results are potentially applicable to a broad range of species and sites. Analyses of the observed patterns of patch occupancy at Bodie revealed little evidence of rescue effects and strong evidence that most recolonizations are ephemeral in nature. Persistence will be overestimated if static or declining patterns of patch occupancy are mistakenly attributed to dynamically stable metapopulation processes. Consequently, simple patch occupancy surveys should not be considered as substitutes for detailed experimental tests of hypothesized population processes, particularly when conservation concerns are involved.

**Keywords:** dispersal, colonization, extinction, metapopulation, pikas, rescue effect.

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Snapshot surveys of the pattern of patch occupancy have been used to infer the existence of balanced metapopulation dynamics in a variety of small and medium-sized mammals (e.g., Smith 1974a; Gottfried 1979; Hanski 1986; Lomolino 1986, 1993; Laurance 1990; Lawton and Woodroffe 1991; Peltonen and Hanski 1991; Weddell 1991; Lindenmayer et al. 1999; Lawes et al. 2000) as well as plants, insects, and birds (Hanski 1998). In many cases, there is little or no direct evidence regarding the role of dispersal in the population dynamics of the species in question. Nonetheless, if isolation predicts the pattern of patch occupancy, this is generally interpreted as sufficient evidence that dispersal is the process responsible. The results from such surveys are then often used to parameterize an incidence function model (IFM) of patch occupancy (Hanski 1994a, 1994b, 1998). While older IFMs did not consider spatial location, part of the appeal of more recent IFMs is that information on spatial location is directly incorporated (Moilanen et al. 1998).

Most spatially explicit recent IFMs are built around two central assumptions: recolonization is distance-dependent, while the probability of patch extinction is unrelated to spatial location (Hanski 1994a, 1994b, 1998). Some IFMs modify the second assumption to reflect the fact that if the rate of recolonization (dispersal to unoccupied patches) is distance-dependent, so too must be the rate of immigration (dispersal to occupied patches), and if immigrants help rescue populations from extinction, more isolated patches will be more likely to become extinct than less isolated patches (Moilanen et al. 1998). Thus, even when the probability of extinction is made contingent on location, the process responsible for generating the spatial pattern of patch occupancy is still assumed to be dispersal.

There are, of course, many processes capable of generating spatial patterns of patch occupancy, independent of any aspect of dispersal. Extinctions may be spatially correlated because of the localized effects of adverse weather, anthropogenic disturbances, or heterogeneity in the pattern of predation. Small mammal ecologists have debated whether dispersal or predation plays the principal part in the population dynamics of their study species for

almost 80 yr (Chitty 1996). Recently, increasingly elegant experiments on ever larger scales have demonstrated the pivotal role of predation (Krebs et al. 1995; Klemola et al. 2000). Avian (Newton 1979; Ydenberg 1987) and mammalian (Peters 1983) predators almost invariably have foraging ranges that are at least one order (and are often many orders) of magnitude greater than that of their small mammal prey. Consequently, the predator's range will often overlap several prey patches simultaneously. In addition, even apparently specialized terrestrial vertebrate predators are able to switch to alternate prey when they have locally extirpated their principal prey (e.g., O'Donoghue et al. 1998). Thus, spatial heterogeneity in the distribution or hunting efficiency of predators likely often causes spatially correlated extinctions in small mammal prey (e.g., Kavanagh 1988; Lawton and Woodroffe 1991; Keith et al. 1993).

Extinctions may also be spatially correlated as a direct (rather than inverse, as with the "rescue effect") result of distance-dependent dispersal. In mammals, immigrants often have detrimental effects on recipient populations (Clinchy 1997). More generally, if most recolonizations are ephemeral, the spatially correlated pattern of recolonizations will later appear as a spatially correlated pattern of extinctions. There are several reasons why most recolonizations are likely to be ephemeral. Since most newly colonized patches likely possess only very small populations, there is a high probability of extinction due to demographic stochasticity. More importantly, with respect to vertebrates, since most dispersal involves juveniles only (Greenwood 1980) and juvenile survival is almost invariably poorer than that of adults (Sibley et al. 1997), newly colonized patches will likely possess populations composed entirely of juveniles that are much more likely to become extinct than a similarly sized population of adults. In mammals, most dispersers are male (Greenwood 1980), and newly colonized patches are likely to contain all male populations (e.g., Gottfried 1979) that are inevitably doomed to extinction.

To establish whether conventional metapopulation processes can legitimately be inferred from a single snapshot of the pattern of patch occupancy, it is critical to first test whether the same pattern of patch occupancy could result from other plausible alternative scenarios, the simplest of which is that the observed pattern of patch occupancy is the product of a unique colonization event followed by successive correlated extinctions. Recolonization is then unrelated to spatial location because either it does not occur or it is effectively negligible. Such a scenario is analogous to the kind of nonequilibrium processes in island biogeography that are thought to provide the best explanation for the current distribution of mammals on both mountaintops (Brown 1971) and oceanic islands (Lawlor

1986; Burbidge et al. 1997). If the very same pattern of patch occupancy that is cited as evidence of the preeminent importance of dispersal in metapopulation dynamics can be produced as easily in the absence of dispersal, then it is clearly not appropriate to infer the existence of metapopulation processes from any single snapshot of the pattern of patch occupancy.

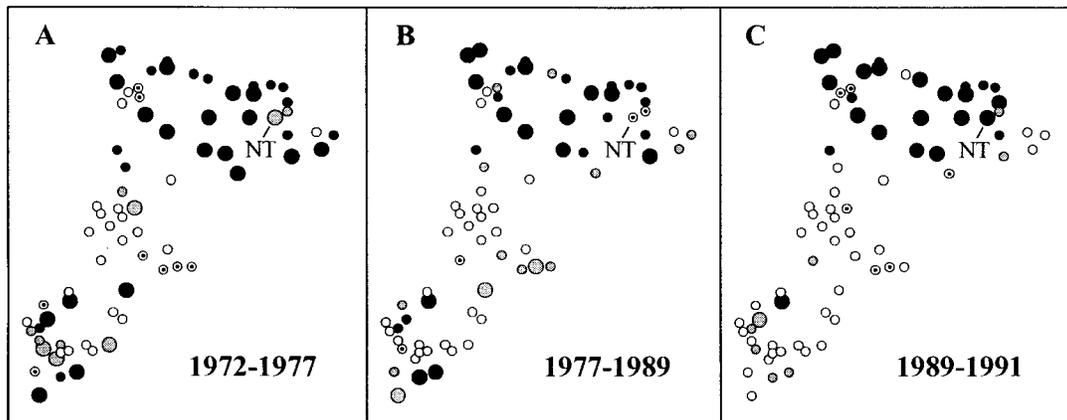
Multiple surveys of the pattern of patch occupancy that demonstrate the existence of recolonization events would appear to invalidate the aforementioned alternative scenario. Moreover, if the number of extinctions and recolonizations is roughly equal, this would appear to be sufficient evidence of equilibrium metapopulation dynamics. However, just such an apparent balance will result if most recolonizations are ephemeral, and this may act to mask the underlying long-term decline inherent in the aforementioned alternative scenario (i.e., successive extinctions following a unique colonization event).

Smith's (1974a, 1980; Smith and Gilpin 1997) long-term study of American pikas (*Ochotona princeps*) at Bodie, California, has been called "the best-known mammalian example of a classical metapopulation" (Moilanen et al. 1998, p. 530). Moreover, it has been suggested that this study provides "some of the best evidence available that [immigration] within mammalian metapopulations can ... rescue local populations from extinction" (Stacey et al. 1997, p. 283).

Contrary to inferences drawn from the several surveys of patch occupancy at Bodie, most detailed behavioral and life-history studies suggest that pikas are remarkably sedentary (Smith 1987). Indeed, despite intensive efforts to directly measure dispersal at Bodie, there have been to date only five direct and eight putative (DNA evidence) cases recorded in which juveniles were observed on other than their natal patch (Peacock and Smith 1997; Smith and Gilpin 1997).

Smith and Gilpin (1997, p. 426) suggested that spatially "correlated extinctions," attributable to predation by weasels (*Mustela frenata* and *Mustela erminea*), may represent an alternative to distance-dependent dispersal, as regards the mechanism (or process) responsible for the observed patterns of patch occupancy among the pikas at Bodie. Independently, Clinchy (1997) argued that spatially correlated extinctions may also explain apparent rescue effects. However, neither article quantitatively evaluated these alternatives.

In this article, we use simulation models to demonstrate that spatially correlated extinctions are sufficient to explain the observed pattern of patch occupancy at the time of any single survey of the pikas at Bodie as well as most observed changes in the patterns of patch occupancy in the intervals between surveys that are generally ascribed to the rescue of local populations by immigration. We also



**Figure 1:** Schematic illustration of the patterns of patch occupancy in successive surveys of the pikas at Bodie. Each panel represents an area of approximately 1,000 ha. Black circles indicate patches that were occupied in both of two successive surveys. Open circles without dots represent patches that were unoccupied in both of two successive surveys. Gray circles signify patches that became extinct in the interval between successive surveys. Open circles with dots indicate patches that were recolonized in the interval between successive surveys. Larger black and gray circles signify patches possessing three or more pikas in the first (initial) of two successive surveys. *NT* = location of the only “nontrivial” extinction-recolonization event (see “Discussion” for details).

report the results of analyses of the changes in patch occupancy and abundance in the intervals between the several surveys at Bodie that indicate that there is little evidence of local populations being rescued from extinction by immigration, strong evidence that most recolonizations are ephemeral in nature, and an overall pattern of population decline. Our goal in conducting the simulations was not to construct the most realistic of models but rather to see whether the simplest of alternatives sufficed to explain the observed patterns. We argue that since the observed patterns of patch occupancy at Bodie are consistent with that expected given both conventional metapopulation processes (e.g., Moilanen et al. 1998) and our alternative scenario, data of a different type than simple patch occupancy surveys are clearly necessary to unambiguously identify the relevant processes.

## Methods

### *Static Pattern of Patch Occupancy at the Time of Each Single Survey*

Four visual surveys were conducted (in 1972, 1977, 1989, and 1991) of the presence and abundance of pikas on 74 anthropogenically created habitat patches near the abandoned mining town of Bodie, California (for details see Smith 1974a, 1974b; Smith and Gilpin 1997). All of the patches are composed of ore dumps left over from excavations begun in 1859 (Smith and Gilpin 1997). There are no records of how the pikas originally came to occupy the ore dumps, but it has been suggested that miners car-

ried them around (purposely or by accident). Prior research conducted in the mid-1940s suggested that all of the patches at Bodie have at one time been occupied by pikas (Smith and Gilpin 1997). When the first survey considered here was conducted, 58% of the patches were occupied (*black and gray circles*, fig. 1A).

If, as assumed by most spatially explicit IFMs, extinctions occur randomly with respect to location and the probability of recolonization is distance-dependent, then in any given survey, more isolated patches are more likely to be unoccupied. This is the principal pattern used to infer the existence of conventional metapopulation processes both among the pikas at Bodie (table 1 in Smith and Gilpin 1997) and in most patch occupancy studies of small and medium-sized mammals. Smith (1974a, 1980; Smith and Gilpin 1997, p. 413) defined patch isolation as the linear distance to the nearest occupied patch with three or more pikas, on the basis that patches “with fewer animals were unlikely to be sources of colonizing individuals.” The more common approach is to simply measure the linear distance to the nearest occupied patch per se (i.e., with one or more individuals). Whether or not patch isolation at Bodie is judged by the distance to the nearest occupied patch with one or more or three or more pikas at the time of each single survey, more isolated patches were significantly more likely to be unoccupied (fig. 1; table 1).

For the sake of generality, we consider only the simplest index of isolation in our simulations, namely, the linear distance to the nearest occupied patch with one or more individuals. In our analyses of the changes in patch oc-

**Table 1:** Results of tests comparing whether unoccupied patches were more isolated than occupied patches at the time of each single survey of the Bodie site

Year/state	Patches (no.)	$\geq 1$ pikas <sup>a</sup>			$\geq 3$ pikas <sup>b</sup>		
		Median	<i>U</i>	<i>P</i>	Median	<i>U</i>	<i>P</i>
1972:							
Occupied	44	42.9	385.5	.003	66.9	378.0	.002
Unoccupied	30	60.8			148.2		
1977:							
Occupied	42	42.9	356.5	.001	80.5	225.5	<.001
Unoccupied	32	62.9			235.6		
1989:							
Occupied	32	44.5	339.5	<.001	60.8	274.5	<.001
Unoccupied	42	75.2			243.2		
1991:							
Occupied	30	39.4	272.5	<.001	63.8	139.5	<.001
Unoccupied	44	104.3			1103.3		

<sup>a</sup> Distance (m) to the nearest occupied patch with one or more pikas.

<sup>b</sup> Distance (m) to the nearest occupied patch with three or more pikas.

cupancy and abundance in the intervals between the surveys at Bodie, we report results judging isolation by the linear distance to the nearest occupied patch with both one or more and three or more pikas. Metapopulation models often estimate patch isolation based on the sum of weighted distances to all occupied patches, rather than just the nearest one. While this seems more realistic, our primary concern over the frequent invocation of metapopulation interpretations of patch occupancy data stems from the fact that so little is generally known about the dispersal process, let alone the level of detail (e.g., Do animals stop when they reach the first available patch? Does survival vary with the distance traveled? etc.) required to adequately estimate the parameter by which dispersal distances are to be weighted (e.g., Moilanen et al. 1998).

#### *Simulations of the Spatially Correlated Extinction Process*

To simulate the effects of spatially correlated extinctions at Bodie, we began by identifying the smallest circle that encompassed all of the patches as our target area (*dashed circle*, fig. 2). We simulated the effect of a predator that extirpated every prey patch (*small, black, or open circles*, fig. 2) within its foraging range by defining disks (*larger open circles*, fig. 2) of varying sizes (reflective of potential differences in foraging areas) measured as a percentage of the total target area (e.g., 0.5%, 5%, and 10%). Since all of the patches at Bodie appear to have at one time been occupied, we began our simulations by assuming that all patches were occupied. Disks were then located randomly and sequentially within the target area, representative of a series of predator-induced extinction events. Every occupied patch within the disk was declared extinct (*smaller*

*open circles*, fig. 2), while those outside the disk remained extant (*small black circles*, fig. 2). All patches were assumed to be equally vulnerable to extinction, regardless of the number of pikas present. Given that an efficient predator, such as a weasel, could readily extirpate a dozen pikas (Ivins and Smith 1983) and that with one exception (the “High Peak” patch, Smith and Gilpin 1997), there were never more than 11 pikas per patch, virtually all patches at Bodie were equally vulnerable. Once a patch was declared extinct, it remained extinct. Recolonization was assumed to be actually or effectively nonexistent; the model did not explicitly address any other demographic process. To validate that the results of our simulations were the consequence of spatially correlated extinctions, we ran additional simulations in which disk size was set to near zero. In this case, only a single patch could be affected in any given extinction event, making extinctions spatially independent.

To ensure that the results of our simulations were not contingent on the specific configuration of patches unique to Bodie, we created target areas in which 74 patches were either randomly and independently located (using a single two-dimensional Poisson process) or moderately or tightly clustered (using a different double Poisson process; Stoyan and Stoyan 1994). Extinction disk simulations were then run as in the Bodie case. We simulated extinction events for each of four disk sizes ( $\cong 0\%$ , 0.5%, 5%, and 10%) using both the Bodie patch configuration and each of our artificially created patch configurations.

To determine the probability with which prior spatially correlated extinctions could explain the observed pattern of patch occupancy at the time of any single survey (e.g., table 1), we calculated the proportion of times unoccupied patches (*smaller open circles*, fig. 2A) were found to be

significantly more isolated than occupied patches (*small black circles*, fig. 2A) across each 10% increment in the proportion of patches unoccupied (e.g., when 15%–25% of all patches were unoccupied, when 25%–35% were unoccupied, and so forth, up to 75%–85%) and then averaged over these ranges (table 2). Simulations were conducted until each percentile range included at least 500 different simulations in which patch occupancy was reduced from 100% down to a value within the specified percentile range. The range of patch occupancies reported varies between 15% and 85% because we used the *t*-test approximation of the Mann-Whitney *U*-test (Sokal and Rohlf 1995) to test for differences in the distributions of distances, which requires a sample of  $\geq 10$  patches ( $10/74 \cong 15\%$ ) in each distribution.

#### Changes in Patch Occupancy in the Interval between Surveys

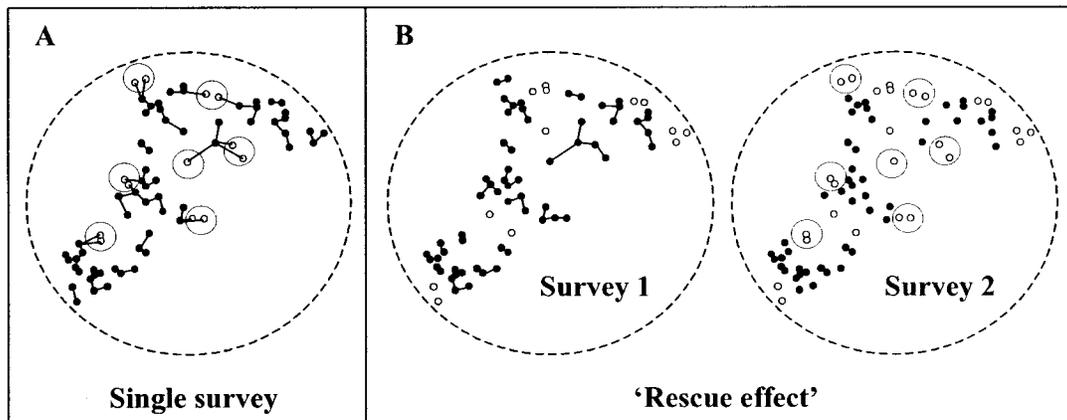
Whenever two or more surveys of patch occupancy are conducted, both the static pattern of patch occupancy at the time of each single survey and the changes in patch occupancy in the interval between the surveys can be examined for evidence of metapopulation processes. Although the pattern of observed changes in patch occupancy would appear to provide the better measure of the underlying dynamics, analyses of such changes are rarely reported.

**Table 2:** Average proportion of times unoccupied patches were found to be significantly more isolated than occupied patches at the time of any single survey as a result of a simulated series of spatially correlated extinction events (as illustrated in fig. 2A)

Patch configuration	Size of extinction disk <sup>a</sup>			
	$\cong .0$	.5	5.0	10.0
Bodie	.02	.68	.97	.98
Random	.03	.37	.96	.99
Moderately clustered	.06	.66	.98	.99
Tightly clustered	.05	.85	.98	.98

<sup>a</sup> Percentage of the total target area.

If at least two surveys are conducted, the observed changes in patch occupancy can be compared with the pattern of changes predicted given either rescue effects or distance-dependent recolonization. If the proximity of other occupied patches reduces the probability of extinction, as predicted by the rescue effect, then patches that become extinct in the interval between any two surveys should be more isolated in the initial survey than patches that remain extant. We determined the probability with which this same pattern could be the result of spatially correlated extinctions events (*larger open circles*, fig. 2B) rather than distance-dependent immigration as assumed by the rescue effect, using data from the simulations discussed in “Simulations of the Spatially Correlated Extinction Process.” In this case, we calculated the proportion



**Figure 2:** Schematic illustration of the extinction disk process. Small circles represent patches; black circles indicate occupied patches, while open circles signify unoccupied patches. The dashed circle represents the “target area,” which is the smallest circle capable of encompassing all of the patches. Extinction disks (*larger open circles*), which are measured as a percentage of the total target area, are randomly located within the target area. Patches within the disks are declared extinct, while those outside the disks remain extant. A, Lines signify the distance between every patch (whether occupied or unoccupied) and its nearest occupied neighbor at the time of any single survey. Extinctions are assumed to have occurred prior to the survey. B, Lines signify nearest neighbor distances between occupied patches only (*small black circles*) in an initial survey (survey 1). Extinctions then occur in the interval between surveys, and the nearest occupied neighbor distances in the initial survey (survey 1) are compared between patches that became extinct (*smaller open circles enclosed in larger open circles in survey 2*) and those that remained extant (*small black circles in survey 2*).

of times patches declared extinct after each extinction event (*smaller open circles enclosed in larger open circles in survey 2, fig. 2B*) were found to be significantly more isolated prior to the extinction event (survey 1, fig. 2B) than patches that remained extant following the extinction event (*small black circles in survey 2, fig. 2B*).

To test whether the observed changes in patch occupancy and abundance in the intervals between the surveys at Bodie corresponded with those predicted by the rescue effect, we first compared whether patches that became extinct in the interval between each pair of successive surveys (*gray circles, fig. 1*) were significantly more isolated in the initial survey than patches that remained extant (*black circles, fig. 1*). Because the rescue effect assumes that population size is "propped up" by the greater exchange of immigrants between nearer patches (Hanski and Gilpin 1997, p. 213), it follows that more isolated patches are more likely to demonstrate population losses. Consequently, we also tested whether the change in the number of pikas on a patch in the interval between each pair of successive surveys was correlated with the patch's degree of isolation in the initial survey. Since immigration entails the addition of individuals to an extant population, only patches that were occupied in the initial survey were included in the correlation. Previous tests for the presence of rescue effects among the pikas at Bodie have been based on the percentage saturation of the available habitat in a given survey (Smith 1980, p. 9; Smith and Gilpin 1997) rather than the actual change in patch occupancy or number of pikas per patch between surveys.

All spatially explicit metapopulation models assume that recolonization is distance-dependent. Consequently, recolonized patches ought to be nearer to their nearest occupied neighbor than those patches that remain unoccupied. We tested whether this was true of the pikas at Bodie by comparing whether patches that were recolonized in the interval between each pair of successive surveys (*open circles with dots, fig. 1*) were significantly less isolated (i.e., nearer to their nearest occupied neighbor; *black or gray circles, fig. 1*) than those patches that remained unused (*open circles without dots, fig. 1*). If recolonizations are largely ephemeral, the pattern of recolonizations will reflect only the most recent dispersal events. If the interval between surveys is longer than the average survival time of such ephemerally occupied patches, the pattern of recolonization will then more closely reflect the pattern of patch occupancy at the time of the second (subsequent) survey (*black circles only, fig. 1*) rather than that at the time of the first (initial) survey (*black and gray circles, fig. 1*).

If at least three surveys are conducted, the observed changes in patch occupancy in the intervals between the surveys can be used to test whether recolonization and extinction are independent of one another, as assumed by

most spatially explicit recent IFMs. While the probability of extinction may be made contingent on spatial location in some spatially explicit IFMs to reflect potential rescue effects, the probability of extinction is nonetheless assumed to be entirely independent of the prior history of recolonization of the patch in question. This assumption is violated if most recolonizations are ephemeral, and extinctions are therefore a direct result of recolonizations. To evaluate whether this was the case among the pikas at Bodie, we conducted a log-linear analysis of the frequency with which extinctions (*gray circles, fig. 1B, 1C*) occurred among patches that were recolonized in the interval between the preceding two surveys (*open circles with dots, fig. 1A*, if considering extinctions in fig. 1B; *open circles with dots, fig. 1B*, if considering extinctions in fig. 1C), as compared to patches that were extant in both of the preceding two surveys (*black circles, fig. 1A*, if considering extinctions in fig. 1B; *black circles, fig. 1B*, if considering extinctions in fig. 1C).

## Results

### *Simulations*

Table 2 summarizes the probabilities, based on our simulations, that at the time of any single survey, unoccupied patches will be found to be significantly farther (i.e., more isolated) from their nearest occupied neighbor than occupied patches are as a result of prior spatially correlated extinction events (fig. 2A). When extinctions were assumed to be independent of one another (disk size  $\cong 0\%$ ), unoccupied patches were significantly more isolated 2%–6% of the time, as would be expected of random results from a one-tailed ( $\alpha = 0.025$ ) test, indicating that our simulations were not intrinsically biased. Even when disk size was only 0.5% of the target area, unoccupied patches were significantly more isolated 68% of the time, given the Bodie patch configuration. Since only those patches that were fairly close together could be extirpated by these very small extinction disks, whether unoccupied patches were significantly more isolated was strongly influenced by patch configuration. However, when the size of the disks was increased to 5% or 10% of the target area, unoccupied patches were significantly more isolated >95% of the time, regardless of patch configuration.

Table 3 summarizes the probabilities based on our simulations that as a result of spatially correlated extinction events, patches that become extinct in the interval between any two surveys will be found to have been significantly more isolated in the initial survey than patches that remain extant (fig. 2B). If the area affected by each extinction disk is very small (0.5% of the target area), spatially correlated extinction events clearly do not provide an adequate ex-

**Table 3:** Average proportion of times patches declared extinct in the interval between surveys were found to be significantly more isolated in the initial survey than patches that remained extant, as a result of a simulated series of spatially correlated extinction events (as illustrated in fig. 2B)

Patch configuration	Size of extinction disk <sup>a</sup>			
	≅.0	.5	5.0	10.0
Bodie	.02	.04	.47	.59
Random	.03	.01	.26	.43
Moderately clustered	.06	.04	.38	.55
Tightly clustered	.05	.09	.52	.60

<sup>a</sup> Percentage of the total target area.

planation if more isolated patches suffer more extinctions. However, when the area affected by each extinction disk was increased to 5% or 10% of the total target area, isolated patches were significantly more likely to become extinct, between 26% and 60% of the time, indicating that spatially correlated extinctions may be responsible in many cases for changes in patch occupancy that are generally ascribed to the rescue of local populations by immigration.

#### Observed Changes in Patch Occupancy and Abundance among the Pikas at Bodie

Patches that became extinct in the intervals between the surveys at Bodie (*gray circles*, fig. 1) were not significantly more isolated than those that remained extant (*black circles*, fig. 1) when isolation was judged by the distance to the nearest occupied patch with one or more pikas (table 4). The same was true when isolation was judged by the distance to the nearest occupied patch with three or more pikas, except for the interval between the third and fourth surveys (1989–1991; table 4). The fact that more isolated

patches were no more likely to demonstrate population losses, regardless of the index of isolation (table 5), confirms that there is little evidence of rescue effects occurring among the pikas at Bodie.

Patches that were recolonized in the intervals between the surveys at Bodie (*open circles with dots*, fig. 1) were significantly less isolated than those patches that remained unoccupied (*open circles without dots*, fig. 1; table 6) only when judged by the pattern of patch occupancy at the time of the second (subsequent) survey (*black circles only*, fig. 1) rather than that at the time of the first (initial) survey (*black and gray circles*, fig. 1). Since the pattern of recolonizations reflects only the most recent dispersal events, most recolonizations are obviously ephemeral in nature.

Whether or not a patch became extinct in the intervals between the surveys at Bodie was very much dependent upon its prior history of recolonization. Recently recolonized patches (*open circles with dots*, fig. 1A, 1B) were significantly more likely to be extinct (table 7; partial  $\chi_1^2 = 16.83$ ,  $P < .001$ ; marginal  $\chi_1^2 = 17.14$ ,  $P < .001$ ), in the subsequent survey (*gray circles*, fig. 1B, 1C) than patches that were occupied in both of the preceding two surveys (*black circles*, fig. 1A, 1B).

#### Discussion

Our simulations demonstrate that the pattern of patch occupancy typically cited as evidence of the preeminent importance of dispersal in metapopulation dynamics (table 1) can be as easily produced by spatially correlated extinctions in the absence of dispersal (table 2). Moreover, changes in patch occupancy between surveys that are typically ascribed to the rescue effect also can be readily produced by spatially correlated extinctions in the absence of dispersal (table 3).

**Table 4:** Results of tests comparing whether patches that became extinct in the interval between each pair of successive surveys at Bodie were more isolated in the initial survey than those that remained extant

Interval/fate	Patches (no.)	≥1 pikas <sup>a</sup>			≥3 pikas <sup>b</sup>		
		Median	<i>U</i>	<i>P</i>	Median	<i>U</i>	<i>P</i>
1972–1977:							
Extinct	10	35.8	126.0	.218	114.0	142.0	.432
Extant	34	47.2			63.8		
1977–1989:							
Extinct	14	47.5	154.5	.268	115.5	166.5	.430
Extant	28	41.3			66.9		
1989–1991:							
Extinct	8	42.9	93.5	.913	196.0	33.0	.006
Extant	24	46.1			48.6		

Note: Results from the initial survey.

<sup>a</sup> Distance (m) to the nearest occupied patch with one or more pikas in the initial survey.

<sup>b</sup> Distance (m) to the nearest occupied patch with three or more pikas in the initial survey.

**Table 5:** Change in the number of pikas on a patch in the interval between each pair of successive surveys at Bodie compared against that patch's degree of isolation in the initial survey

Interval	Initially occupied patches (no.)	$\geq 1$ pikas <sup>a</sup>		$\geq 3$ pikas <sup>b</sup>	
		Spearman's <i>r</i>	<i>P</i>	Spearman's <i>r</i>	<i>P</i>
1972–1977	44	.09	.570	.08	.619
1977–1989	42	-.21	.175	-.12	.454
1989–1991	32	-.08	.666	-.17	.349

Note: Results from the initial survey. Only patches that were occupied in the initial survey were included in the correlation to reflect the fact that immigration entails the addition of new individuals to extant populations

<sup>a</sup> Distance (m) to the nearest occupied patch with one or more pikas in the initial survey.

<sup>b</sup> Distance (m) to the nearest occupied patch with three or more pikas in the initial survey.

Consistent with the cause being some spatially correlated process, extinctions at Bodie (*gray circles*, fig. 1) have tended to occur in clusters (cf. fig. 2A). Smith and Gilpin (1997, p. 426) suggested that “it is likely that weasel predation is the most common cause of extinction of a population of pikas on a patch.” Our analyses (table 7) clearly indicate that recolonization is also, in effect, a common cause of extinction. An average weasel home range (10–16 ha; Burt and Grossenheider 1976) encompasses 1.6% of the total Bodie target area (fig. 2). Using a disk size of 1.6%, there is a 91% likelihood that in any given survey

of the Bodie site unoccupied patches will be found to be significantly more isolated (see table 2) and a 19% likelihood that patches that become extinct in the interval between surveys will be found to have been significantly more isolated in the initial survey (see table 3). Weasel predation alone or in combination with other spatially correlated causes of extinction (e.g., recolonization) is clearly capable of generating the observed patterns of patch occupancy reported in table 1.

We conducted six tests (table 4) of whether the observed changes in patch occupancy in the intervals between the several surveys at Bodie were consistent with the rescue effect. Only one of these six tests was significant (table 4). We suggest this result may be a prime example of how a series of spatially correlated extinction events can generate just such a change in patch occupancy. It is evident from figure 1 that extinctions (*gray circles*) occurred more often in the southern portion of the site. While there had been eight patches with three or more pikas in the southern portion of the site in 1972 (*larger black and gray circles*, fig. 1A), there were only two such patches remaining in 1989 (fig. 1C). As was true of the preceding two intervals (fig. 1A, 1B), most (six out of eight) of those patches that became extinct between 1989 and 1991 (*gray circles*, fig. 1C) were in the southern portion of the site. Thus, as a result of a prior and continuing preponderance of extinctions in the south, there was an inverse relationship between the frequency of extinctions (mostly in the south;

**Table 6:** Results of tests comparing whether patches that were recolonized in the interval between each pair of successive surveys at Bodie were less isolated than those that remained unused as judged by the pattern of patch occupancy in the first (initial) or second (subsequent) of each pair of successive surveys

Interval/fate	Patches (no.)	Pattern <sup>a</sup>	$\geq 1$ pikas <sup>b</sup>			$\geq 3$ pikas <sup>c</sup>		
			Median	<i>U</i>	<i>P</i>	Median	<i>U</i>	<i>P</i>
1972–1977:								
Recolonized	8	1972	77.9	62.0	.223	245.8	71.0	.425
Unused	22		60.4			147.4		
Recolonized	8	1977	36.2	29.0	.006	44.1	32.5	.009
Unused	22		66.5			228.0		
1977–1989:								
Recolonized	4	1977	50.7	37.0	.279	212.8	54.5	.932
Unused	28		64.7			250.8		
Recolonized	4	1989	43.2	38.5	.319	89.7	25.5	.082
Unused	28		76.1			243.2		
1989–1991:								
Recolonized	6	1989	105.9	95.5	.653	197.6	106.5	.957
Unused	36		75.2			243.2		
Recolonized	6	1991	36.6	50.5	.039	288.8	49.5	.035
Unused	36		100.1			975.7		

<sup>a</sup> Distances measured in relation to the pattern of patch occupancy in the specified year.

<sup>b</sup> Distance (m) to the nearest occupied patch with one or more pikas.

<sup>c</sup> Distance (m) to the nearest occupied patch with three or more pikas.

**Table 7:** Frequency with which extinctions occurred in the subsequent survey, among patches that were recolonized in the interval between the preceding two surveys at Bodie, as compared to patches that had been occupied in both of the preceding two surveys

Preceding surveys	Recolonized <sup>a</sup>		Occupied <sup>b</sup>	
	Extinct	Extant	Extinct	Extant
1972–1977	7	1	7	27
1977–1989	3	1	5	23

<sup>a</sup> Fate in the subsequent survey of patches recolonized in the interval between the preceding two surveys.

<sup>b</sup> Fate in the subsequent survey of patches occupied in both of the preceding two surveys.

fig. 1C) and the abundance of patches with three or more pikas (mostly in the north; fig. 1C), leading to a pattern of change in patch occupancy (the sole significant result in table 4) that might otherwise be ascribed to the rescue effect.

That the apparent rescue effect reported in table 4 is more likely the result of a spatially correlated pattern of declines and extinctions is all the clearer when the change in the number of pikas on a patch in the interval between successive surveys is compared against the patch's north-south coordinate (i.e., northing; table 8). There was an obvious pattern of cumulative population losses in the southern portion of the Bodie site over the 19-yr period between the first and last surveys (fig. 3).

While many patches became extinct at Bodie (table 4), many were also recolonized (table 6). Overall, the total number of extinctions (32) and recolonizations (18) did not differ significantly from a 1 : 1 ratio (binomial  $P = .065$ ); therefore, the system was technically in equilibrium. Of course, a roughly equivalent number of extinctions and recolonizations is as to be expected if most recolonizations are ephemeral in nature. Notably, the distribution of patches that were recolonized between 1989 and 1991 reflected only the pattern of patch occupancy in 1991 and not that in 1989 (table 6), suggesting that most recolonized patches were extinct within 2 yr. The fact that recently recolonized patches were disproportionately more likely to become extinct is evident from table 7. Recently recolonized patches generally held only one or two pikas (median = 2, range = 1–5). Nonetheless, their greater rate of extinction was not attributable to small population size per se because recently recolonized patches were still significantly (partial  $\chi_1^2 = 8.67$ ,  $P = .003$ ; marginal  $\chi_1^2 = 8.65$ ,  $P = .003$ ) more likely to become extinct than were comparably sized patches ( $N \leq 2$ ) that were occupied in both of the preceding two surveys. Given the disproportionate probability and apparently rapid rate with which recently recolonized patches became extinct, we sug-

gest that this principally reflects the dispersal and death of that year's crop of juveniles.

Smith (1974a, 1980; Smith and Gilpin 1997) argued that patches with less than three pikas are of negligible significance with respect to metapopulation processes. Only two of the 12 patches recolonized between 1972 and 1989 (table 7) were still extant in 1991: one of which had only two pikas on it, while the other (labeled "NT" for "nontrivial" in fig. 1) had four. All of the patches recolonized between 1989 and 1991 had less than three pikas. Consequently, if only those patches with three or more pikas contribute meaningfully to future metapopulation processes, then only one nontrivial extinction-recolonization event can be said to have occurred during the 19-yr period between the first and last surveys at the Bodie site. Recolonization at Bodie, therefore, has been effectively negligible, as assumed by our simple alternative scenario.

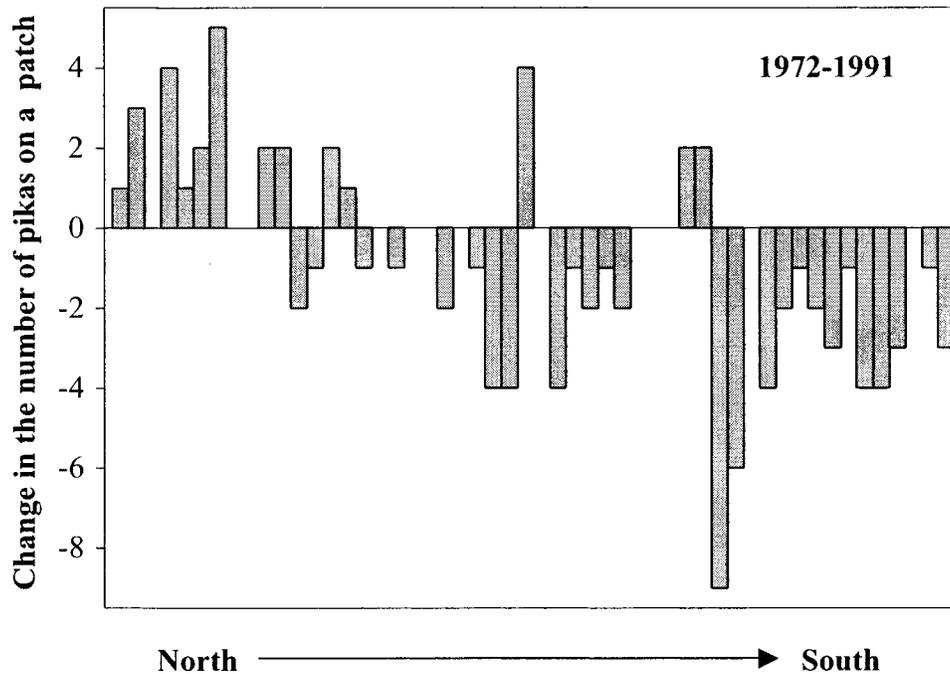
Contrary to the apparent balance between the total number of extinctions and recolonizations noted above, there was a significant decline (1 : 8 vs. 1 : 1; binomial  $P = .039$ ) in the number of "meaningfully sized" patches (those with three or more pikas; larger black or gray circles, fig. 1) between the first and last surveys at Bodie. The decline in patch occupancy (by 32%; table 1) mirrored a proportional decline (by 27%, excluding the High Peak patch) in the total number of pikas censused. Thus, even when multiple surveys of patch occupancy are conducted, an underlying decline in patch occupancy (and population size) may be masked by the correlation in the number of recolonizations and extinctions that is likely to result from the annual dispersal and death of juveniles that is the norm in most vertebrates (Greenwood 1980; Sibley et al. 1997).

We suggest that the progressive decline in patch occupancy at the Bodie site (fig. 1) is consistent with the steady accumulation of extinction events following an earlier colonization period, such as is modeled by our extinction disk simulations (fig. 2; tables 2, 3). Given that the pikas at Bodie represent the classic example of a mammalian

**Table 8:** Change in the number of pikas on a patch in the interval between successive surveys at Bodie compared against that patch's north-south coordinate (i.e., northing)

Interval	Patches (no.)	Spearman's $r$	$P$
1972–1977	52	.12	.400
1977–1989	46	.41	.005
1989–1991	38	.43	.007
1972–1989	46	.60	<.001
1977–1991	45	.67	<.001
1972–1991	49	.64	<.001

Note: Only patches that were occupied in one or both of the two surveys under consideration were included in the correlation.



**Figure 3:** Change in the number of pikas on a patch in the interval between the first and last surveys at the Bodie site compared against that patch's ranked north-south coordinate (i.e., northing). Only patches that were occupied in one or both of the two surveys under consideration are illustrated.

metapopulation, our conclusion is that processes cannot be inferred from simple surveys of the pattern of patch occupancy; data of a different type are clearly necessary.

Our results do not indicate that meaningful metapopulation processes cannot or do not occur. They do call into question just what constitutes sufficient evidence. Smith (1980, p. 8) recognized that there was a dichotomy between studies of dispersal based on census data and "in-depth studies of population dynamics" designed to experimentally test hypothesized population processes. Small mammal ecology, in particular, is replete with experimental studies of dispersal (Krebs 1996). The importance of immigration and recolonization can be experimentally tested by removing part (e.g., Clinchy et al. 2001) or all (Stenseth and Lidicker 1992), respectively, of the resident population. The surest way to determine whether an unoccupied patch (still) represents suitable habitat is to transplant individuals into that patch (while transplanting others within occupied patches) and seeing whether they survive and reproduce (Krebs 2001). While our model assumed weasel predation was the most likely cause of spatially correlated extinctions, this assumption is best tested by conducting a predator (i.e., weasel) exclusion experiment (e.g., Krebs et al. 1995; Klemola et al. 2000).

There is often resistance to conducting in-depth studies

or experiments on threatened species, whereas simple surveys are seen as less invasive alternatives. If, however, simple surveys act to obscure the identification of relevant processes and mask significant population declines, then they are clearly no substitute for in-depth experimental studies of the actual population dynamics.

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