ECOLOGICAL INFLUENCES ON THE DYNAMICS
OF A FIELD VOLE METAPOPULATION

Elizabeth E. Crone,[1] Daniel Doak,[2] and Jouko Pokki[3]

[1]*Ecology Division, Biological Sciences Department, University of Calgary, Calgary, Alberta, Canada T2N 1N4*
[2]*Department of Biology, University of California, Santa Cruz, California 95064 USA*
[3]*Tvärminne Zoological Station, J. A. Palméns Road 260, 10900 Hanko, Finland*

Abstract. Although metapopulation theory is widely used in basic and applied ecology, there are still few empirical studies that explore the relationships between dispersal, patch size, and the persistence of natural populations. Here, we reanalyzed data from a six-year study of a spatially structured field vole (*Microtus agrestis*) metapopulation in the Tvärminne archipelago, Finland. Our goal was to address several issues relevant to metapopulation studies: (1) the relationships between within-subpopulation dynamics, dispersal behavior, habitat quality, and metapopulation dynamics; (2) the generality of one of the most common conclusions of metapopulation theory—that smaller and less frequently inhabited islands are less important for metapopulation dynamics; and (3) the comparison of different methods for understanding and predicting dynamics in ''metapopulation-like'' systems. Our results suggest that this vole metapopulation is driven by extinctions and colonizations of island subpopulations. However, contrary to expectation, colonizations by voles from tiny, ephemeral skerry subpopulations were about as important for metapopulation persistence as were colonizations from the more persistent subpopulations on large islands. This pattern resulted from less stable vole densities on smaller islands, combined with increased emigration preceding subpopulation extinctions. Either spatially implicit Levins models or incidence function models provided reasonable predictions of the structure and function of this metapopulation, but parameters fitted to incidence functions varied dramatically among years. Our results suggest that models of real metapopulations need not become highly detail oriented or spatially complicated to provide good predictive power. However, applications of metapopulation theory require careful consideration of how underlying ecological and behavioral mechanisms will shape metapopulation dynamics of particular species and situations.

Key words: dispersal; extinction; field voles; Finland; incidence function analysis; patch size; population dynamics; metapopulation; Microtus agrestis.

INTRODUCTION

Over the past twenty years, the theory of metapopulation dynamics has become one of the backbones of modern population ecology (e.g., Hanski and Gilpin 1997). Metapopulation ideas also rest at the heart of both the theory and practice of conservation biology (Doak and Mills 1994, Sjögren-Gulve and Ray 1996, With 1997). In particular, while the term ''metapopulation'' is often loosely used to mean essentially any population scattered across noncontinuous habitat patches, the narrow-sense idea of dynamics driven by local extinction and recolonization events (Levins 1970) has come to dominate the conceptual view of spatial population structure in ecology textbooks (Krebs 1994, Gotelli 1995), symposia proceedings (McCullough 1996, Hanski and Gilpin 1997) and journal articles (e.g., Menges 1990, Hanski et al. 1996, Quintana-Ascencio and Menges 1996, Gyllenberg and Hanski 1997). While this still-growing interest in me-

tapopulation processes has led to increasingly sophisticated analyses and the pursuit of ever-better data sets (Hanski 1994*a,* Sjögren-Gulve and Ray 1996, Smith and Gilpin 1997), there is still a paucity of field studies that allow direct tests of some of the key assumptions and outcomes of extinction/recolonization dynamics. Here, we reanalyze a long-term, large scale study of a spatially structured small mammal metapopulation to address several issues important for widespread application of metapopulation theory.

The beauty (and much of the utility) of Levins' metapopulation theory lies in its combined ability to predict metapopulation dynamics at the same time that it ignores many of the details of individual and population ecology. Briefly, the attraction of metapopulation theory is its focus on the qualitative dynamics of subpopulations living on distinct habitat islands or patches. To parameterize a metapopulation model, one need only record the rates of subpopulation extinctions and recolonizations on each habitat island. For the simplest metapopulation models, these rates themselves are the parameters needed to predict the mean occupancy rate of islands. For more complicated models, these rates

are estimated as functions of island size, proximity, patch quality, or other factors, allowing the prediction of patch occupancy rates and extinction probabilities (Hanski 1994a, Hanski et al. 1996, Gyllenberg and Hanski 1997, Holt 1997). Because this approach does not rely upon knowledge of dispersal behavior, records of individual dispersal events, or the following of within-year, within-subpopulation dynamics, it provides a research and monitoring protocol that seems surprisingly doable for many species in many settings.

However, the very simplicity of the metapopulation view of spatial population dynamics may limit how well it explains or predicts most real ecological situations. The behavioral and population processes that drive spatial dynamics are clearly almost always more complex than assumed by metapopulation models. What is not clear is whether these complications will lead to metapopulation patterns that systematically differ from those predicted by simple models. From the perspective of developing metapopulation models, we need to know what, if any, realistic "details" of actual species and populations are necessary to consider when constructing metapopulation models and using them to predict extinction probabilities, effects of habitat loss or creation, and other issues of concern to ecologists or land managers. Nonetheless, few studies that have used a metapopulation framework to explore population dynamics have incorporated detailed studies of within-subpopulation dynamics or individual dispersal behavior to ask what information is lost by taking a simple metapopulation perspective that ignores this detailed information.

In an extensive field study, Pokki (1981) monitored field vole (*Microtus agrestis* L.) behavior, within-island dynamics, and patch turnover dynamics across an island metapopulation in the Tvärminne archipelago, Finland, for six years. Over the course of this study, extinctions and recolonizations of local island subpopulations were common. Reanalyzing published and unpublished data from Pokki's study, we address three key issues in metapopulation analysis:

1) How important is consideration of within-subpopulation dynamics to an understanding of metapopulation dynamics?
2) Does individual behavior complicate an otherwise simple metapopulation scenario?
3) How robust is one of the most common generalities of metapopulation theory: smaller and less frequently inhabited islands are less important for overall metapopulation dynamics?

In addressing these questions, we use a combination of simple, "spatially implicit" metapopulation models, incidence function models (Hanski 1994a), and predictions of net dispersal built from direct measurements of vole dispersal and abundance, leading to comparisons of the reliability of these approaches in understanding and predicting metapopulation behavior.

Study System and Field Data

The Tvärminne Archipelago is located in the Gulf of Finland, just off the southernmost coast of Finland, ~100 km west of Helsinki. In this area, the boundary between land and sea is a graded archipelago of thousands of islands. The innermost islands are large and wooded, with only narrow strips of water between them, but outer islands are generally small, widely scattered, treeless skerries. The field vole (*Microtus agrestis* L.) is the most common small mammal in the outer parts of this archipelago, and on the outermost skerries it is usually the only mammal species present (Pokki 1981).

From 1972 to 1977, J. Pokki monitored field vole populations on a set of 71 islands, near the Tvärminne Zoological Station, where the archipelago is at its narrowest, only ~3 km wide from the mainland to the outermost skerries (Fig. 1). Pokki (1981) divided islands into three size classes: large islands (>5 ha), medium islands (1–5 ha), and small skerries (<1 ha). To understand the basic mechanisms regulating vole dynamics on these islands, Pokki followed behavior and distribution using monthly censuses and a combination of live trapping, snap trapping, and visual inspection for vole feces or vegetation cuttings (typical of vole foraging; Pokki 1981). While limited snap trapping was carried out on at least some islands in each year, the demographic effects of this sampling appeared to be negligible (see discussion in Pokki 1981: 14). Over the course of the study, age, sex, reproductive status, and location were recorded for >2000 marked individual voles.

Pokki's study revealed several key features of this metapopulation. First, seasonal dynamics varied with island size. On treeless skerries, vole abundance mirrored development of vegetation. Vole populations grew during the early summer flush of vegetative growth, and voles on skerries had higher maturation rates, litter sizes, and mean densities than on larger islands during this period. However, skerry populations declined in late summer when favored plant species were largely consumed, and many plants shifted from vegetative growth to seed production; these declines resulted from both higher mortality and higher emigration (movement to other islands). On large islands, populations peaked in autumn, and voles responded to seasonal crowding by intra-island movement from preferred habitat (old fields and meadows) to suboptimal habitat (heaths and forests), with relatively low rates of inter-island movement.

Second, extinctions and recolonizations of local island subpopulations were common (Table 1). We define an extinction as having occurred when an island was not occupied for an entire summer, after being occupied in the previous year(s); similarly, a recolonization occurred when voles were found on an island previously unoccupied for an entire summer (details of sampling
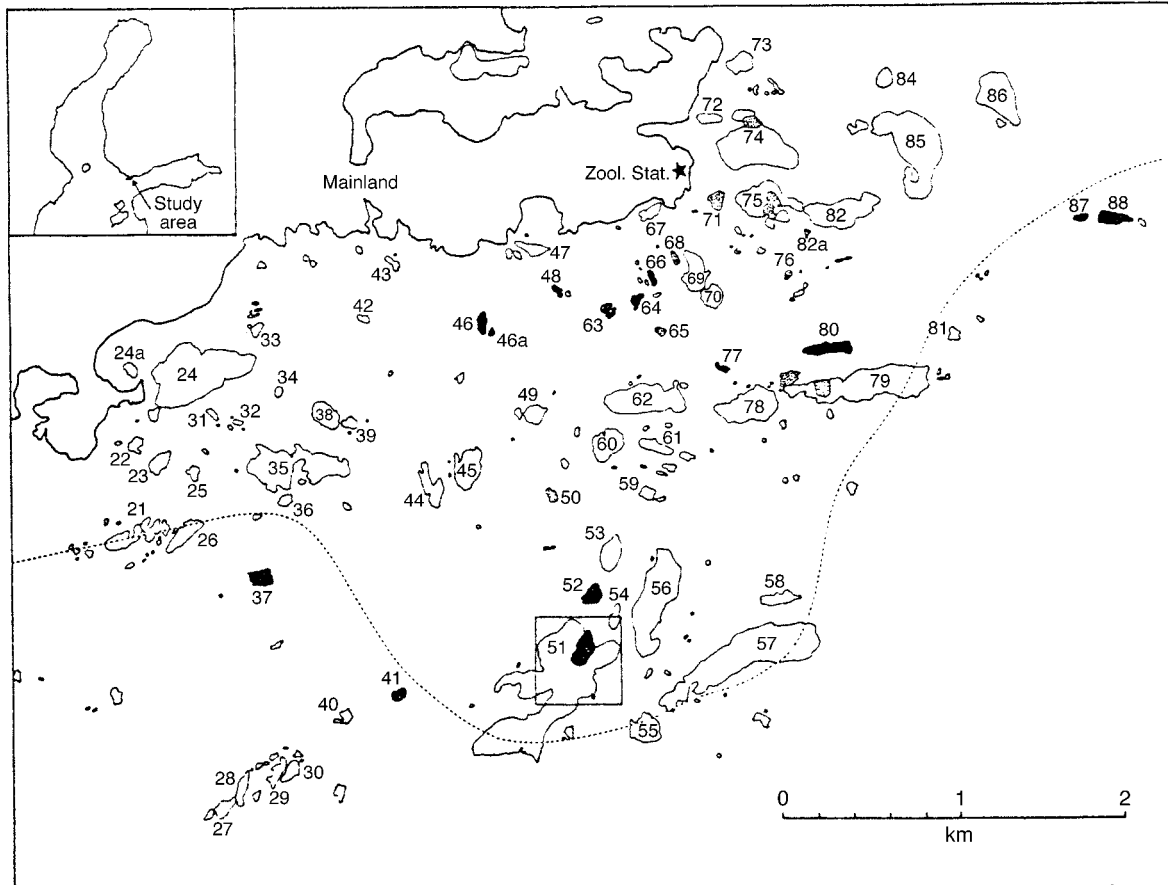
Fig. 1. Map of the Tvärminne archipelago. Numbered islands are those on which vole distribution was monitored from 1972 to 1977. (Figure from Pokki [1981].)

methodology are described by Pokki [1981]). Although extinctions were less common on large than on small islands (Table 1), they were still a major force driving dynamics. Of 13 large islands monitored over six years, only one was continuously occupied by field voles for the entire study period, and seven were uninhabited for at least one entire summer (Pokki 1981). Conversely, while extinctions were more common on skerries, they

TABLE 1. Summary data for the Tvärminne field vole metapopulation, 1972–1977 (from Pokki 1981).

Parameter	Island size		
	Skerry (<1 ha)	Medium (1–5 ha)	Large (>5 ha)
1) Number of islands monitored	40	18	13
2) Total area (ha, summed over islands)	19.7	28.7	121.6
3) Extinctions · (occupied island)$^{-1}$ · yr^{-1}	0.72	0.25	0.20
4) Colonizations · (unoccupied island)$^{-1}$ · yr^{-1}	0.40	0.84	0.82
5) Mean occupancy, 1972–1977	0.42	0.75	0.80
6) Per capita successful dispersal†	0.085	0.025	0.006
	($n = 1037$)	($n = 157$)	($n = 981$)
7) Immigration per island size class‡	0.34	0.21	0.45
8) Litter size (1 SE)§	6.2 (0.2)	⋯	5.3 (0.1)
9) Density (voles/ha)§	103	⋯	78
10) Ecological density (voles/vegetated ha)§‖	1907	⋯	118

† Percentage of voles that were marked on islands and recaptured on other islands. This is an estimate of relative per capita dispersal rates and an absolute minimum estimate of total dispersal rates from islands of each type.

‡ Percentage of recaptured, emigrating voles that dispersed to this island type.

§ Measured on a subsample of seven skerries and one large island.

‖ Ecological density is the maximum number of voles on each island in each year, divided by the area of each island vegetated with suitable habitat for field voles; see Pokki 1981.

were by no means predictable annual cycles: the median period of occupancy for skerries was two years, with a maximum of at least five years (one skerry was occupied throughout the first five years of the six-year monitoring study). On both tiny skerries and large islands, voles at least sometimes successfully overwintered, based on observation of marked voles, high vole abundances on skerries in early spring, and low rates of dispersal in early spring (see also Figs. 7 and 16 in Pokki 1981). However, monthly survivorship of adult voles during the seven winter months was low, averaging between 0.7 and 0.8 (70–80%). Thus, there were probably two important mechanisms of subpopulation extinction: demographic stochasticity driven by low survivorship and small population sizes on all islands, and environmental variability due to low food availability on skerries, driven by annual variation in population density and rainfall.

Finally, Pokki established that voles frequently dispersed among islands. Based on the timing of dispersal (Pokki 1981), most inter-island movement was by swimming. (Field voles released in the Gulf of Finland are capable of swimming >200 m; J. Pokki, *unpublished data*.) Marked voles were far more likely to emigrate from skerries than from larger islands (Table 1), but most often immigrated to larger islands.

In this paper, we draw on two sources of data: published information from Pokki's monograph (Table 1), and unpublished records of occupancy, size, and location for each of the 71 islands in the study region from 1972–1977. Distances between islands were calculated based on the location of island centroids on a 1:10 000 map of the archipelago. (Centroids presumably reflect the mean distance a vole would travel in moving from one island to another.) Distances from each island to the mainland were based on the distance from the island centroid to the nearest point on the shore.

Methods and Results

To understand the dynamics of the Tvärminne vole metapopulation, we test several hypotheses about the nature of extinctions, colonizations, dispersal, and patch occupancy patterns in the metapopulation. For example, Harrison (1991) delineated two variants of classic metapopulations, which Pokki did not consider in his description of the Tvärminne voles: ''nonequilibrium metapopulations'' in which occupancy of a set of habitat patches is gradually declining (or increasing) over time; and ''mainland–island metapopulations'' in which most of the colonization is due to dispersal from a few large ''source'' subpopulations. The hypothesis of mainland–island dynamics is particularly appealing for this population (Harrison and Taylor 1997; see Fig. 1). Pokki did not monitor vole movement to or from the large mainland population, a potentially significant source of dispersing voles. In addition to the question of overall metapopulation pattern, we sought to elu-

cidate the importance of variation in habitat quality and differences in vole dispersal among patches of different sizes (e.g., Gyllenberg and Hanski 1997, Holt 1997). In the analyses that follow, we first address these questions using three different types of spatial modeling approaches: (1) simple metapopulation models, (2) spatial incidence function models, and (3) dispersal models built from individual and subpopulation data. We then consider the implications of these relationships for one of the most common questions asked in application of metapopulation models: (4) how important are different kinds of subpopulations for metapopulation persistence?

Simple metapopulation models: patch heterogeneity and equilibrium dynamics

Methods.—For a simple metapopulation at equilibrium,

$$p_{t+1} = p_t + c(1 - p_t) - dp_t \qquad p^* = \frac{c}{c + e} \quad (1)$$

where p_t is the fraction of patches that are occupied in year t; c and e are directly measured annual, per island colonization and extinction frequencies, respectively (e.g., extinctions and colonizations in Table 1); and p^* is equilibrium patch occupancy (Levins 1970). However, if a metapopulation is not at equilibrium, classic Levins metapopulation dynamics are as follows:

$$p_{t+1} = p_t + mp_t(1 - p_t) - ep_t \qquad p^* = 1 - \frac{e}{m} \quad (2)$$

where m is the rate at which unoccupied patches are colonized per occupied patch per year (henceforth ''colonization rate'', which was not directly measured in Pokki's field data, as opposed to c, which was directly measured), and all other parameters are as defined above (Levins 1970).

Pokki (1981) subjectively divided islands in the Tvärminne archipelago into three size categories, which support different vegetative communities, and have vole subpopulations with differing growth, extinction, dispersal, and immigration rates. In the following section, we consider analyses with island size as a continuous variable. Here, we retain Pokki's original three-size type distinction as a simple and natural extension of the Levins metapopulation formulation. Differences between island types can be incorporated into a Levins metapopulation model as follows:

$$p_{i,t+1} = p_{i,t} + m_i(f_1 p_{1,t} + f_2 p_{2,t} + f_3 p_{3,t})(1 - p_{i,t})$$
$$- e_i p_{i,t} \qquad (3)$$

where $p_{i,t}$ is the fraction of islands in size class i that are occupied in year t, $i = \{1,2,3\}$ for three island size classes, f_i is the fraction of successful colonizations which are due to dispersers from an occupied island of size class i (henceforth ''dispersal fraction''), and e_i and m_i are as defined above. (Theoretical investigations

TABLE 2. Parameters fitted for the size class metapopulation model (Eq. 3), with 90% confidence limits from likelihood profiling.

Island size	Colonization rate (m_i)	Extinction rate (e_i)	Dispersal fraction (f_i)
Big	1.35	0.20	0.12
($n = 13$)	(0.84, 1.83)	(0.11, 0.33)	(0, 1)
Medium	1.12	0.25	0.44
($n = 18$)	(0.85, 1.29)	(0.36, 0.15)	(0, 1)
Skerry	0.83	0.64	0.44
($n = 40$)	(0.53, 1.12)	(0.53, 0.74)	(0, 1)

Note: For extinction and colonization rates, values differ significantly between island size classes.

of structurally similar metapopulation models are presented in Holt 1997).

To fit parameters of this model to the Tvärminne voles, we found maximum likelihood estimates (and confidence limits), based on binomial distributions for extinctions of occupied islands and colonizations of unoccupied islands, combining data from all transitions from 1972–1973 to 1976–1977. For extinctions, rates depended only on the categorical size class variable, with

$$\Pr(\text{extinction} \mid \text{occupied island of type } i) = e_i.$$

To estimate colonizations, we fit three functions, one for each size class:

$$\Pr(colonization \mid unoccupied\ island\ of\ type\ i)$$
$$= \min[1, m_i(f_1 p_{i,t} + f_2 p_{2,t} + f_3 p_{3,t})]$$

with parameters defined as in Eq. 3, with $p_{i,t}$ indicating actual observed occupancy, which varied among years, unlike island size class designations. These colonization functions are piecewise linear, in order to directly reflect Eq. 3. In total, these functions use six parameters (one m and one f for each island size class) to define nine pairwise rates. Ecologically, this means voles leaving from islands of a particular size are assumed to have no bias to disperse to islands of any particular size class.

Results.—The Tvärminne archipelago vole population appears to be a persistent metapopulation. For islands of all three size classes, estimated extinction rates were lower than estimated colonization rates (Table 2), although 90% confidence limits for these parameters overlap somewhat for ephemeral skerry subpopulations. Extinction and colonization parameters differed significantly among islands in different size classes ($N = 150$–420, for three contrasts, with all $P < 0.01$ for likelihood ratio tests against a null model with constant, size-independent e and m), with high colonization and low extinction in large and medium islands, and low colonization and high extinction of small skerries (Table 2). Dispersal fractions could not be bounded statistically, presumably due to small variation in mean island occupancy over the course of the study. How-

ever, maximum likelihood estimates of these parameters suggest that dispersal from large, permanent island subpopulations is far less frequent than dispersal from smaller islands (Table 2), in accord with Pokki's estimates of individual movement rates (Table 1). In general, expected rates of island occupancy based on the size class model match observed occupancy well (Fig. 2A); this is not a surprising result, since the model was fitted to the same data against which it is compared.

While this simple model provides some insight into function, it does not easily allow testing of mainland effects or more careful analysis of island size or position effects. To address these issues, we next develop an incidence function model for the Tvärminne vole metapopulation, and then compare results derived from both methods.

Incidence function model: island area, dispersal, and the mainland

Methods.—Here, we develop a model adapted from Hanski's incidence function approach (Hanski 1994*a, b,* Hanski and Thomas 1994, Hanski et al. 1995, Wahlberg et al. 1996; see also Verboom 1996). Our goals are to test whether the mainland might be the primary source of recolonists for unoccupied islands throughout the archipelago, and to incorporate the possible effects of movement behavior (dispersal biased toward closer islands, expressed as location-dependent occupancy) and within-patch dynamics (more frequent extinctions on smaller islands, expressed as size-dependent occupancy) on metapopulation behavior. Static patterns of island occupancy were fitted with the following model

$$J_{i,t} = \cfrac{1}{1 + \cfrac{\mu}{\left[e^{-\alpha d_{i,\text{mainland}}} A_{\text{mainland}}^b + \sum_{j=1}^{n} \hat{p}_{j,t} e^{-ad_{i,j}} A_j^b \right]^2 A_i^x}}. \quad (4)$$

Observed parameters are: $J_{i,t}$, the probability that island i is occupied at time t; $\hat{p}_{j,t} = 1$ for occupied and 0 for unoccupied islands in year t; $d_{i,j}$, the distance between islands i and j; and A_j, the area of island j. Fitted parameters are: A_{mainland}, the "effective" area of the mainland vole population; $b,$ a fitted model parameter that scales the relationship between island area and its contribution to the group of dispersing voles; α, which scales the effect of distance between islands on inter-island movement; $x,$ which (as defined by Hanski [1994*a*]) represents the relationship between island area and extinction probability; and μ, a scaling parameter (see Hanski et al. 1996). While these heuristic definitions of the fitted parameters are useful, the value of each parameter does not solely reflect effects on colonization or extinction, but rather the combined influences of location or size on occupancy.

Our approach differs from previous applications of incidence function models (e.g., Hanski et al. 1996) in
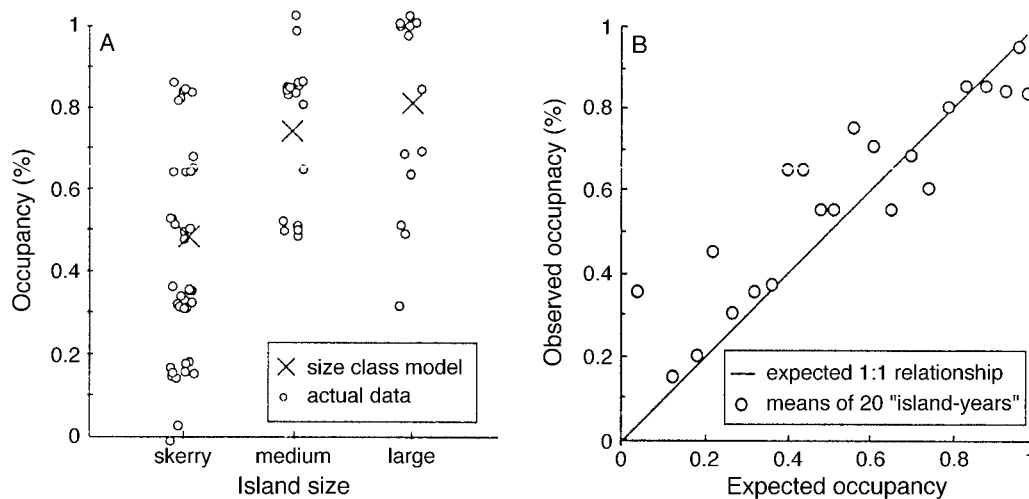
FIG. 2. Observed vs. expected island occupancy. (A) Levins' model expectations (×'s) are equilibria calculated from extinction and colonization rates and the fractions of colonists provided by each size class (Table 2), with actual mean occupancy for each island (circles). (B) Probability of island occupancy, based on the incidence function model, varies for each island in each year, so 426 ''island years'' were ranked by percentage occupancy and grouped into sets of 20, and mean probabilities of occupancy and percentage actual occupancy are shown for each group (circles), relative to expected 1:1 relationship (line).

two ways: (1) the ''effective'' area of the mainland population was fitted as a model parameter, and (2) we explicitly fitted b, the relationship between island size and its contribution to the number of dispersing voles. Previous incidence function analyses assumed fixed, increasing, relationships between island size and dispersal ($b > 0$, typically 0.25 to 1; e.g., Hanski 1994a, Hanski et al. 1996, Quintana-Ascencio and Menges 1996), but Eq. 4 is substantially more able to reflect complex relationships between subpopulation size and dispersal. These modifications allow a variety of relationships between island size, dispersal, and mainland–island dynamics. For example, if large islands are important sources of potential colonists but the mainland is unimportant, then $b > 0$ and $A_{mainland} = 0$. Alternatively, if the mainland population is the only important source of vole colonists in the archipelago, $A_{mainland} \gg \Sigma(A_j^b)$. Finally, if $b > 0$, net contribution to colonization increases with island size, while if $b < 0$, smaller islands provide more colonists.

While the model we present is quite flexible, it uses only one of the near-infinite array of possible sets of functional forms that the incidence function approach could accommodate. We chose this model (and the submodels described below) based upon visual exploration of the fit of a much broader array of models to our data, and the criteria that a model must lead to stable parameter estimates when fit to occupancy data (i.e., convergent maximum likelihood estimates). For example, we rejected the idea of fitting a single model to all years of data because several, widely different, parameter sets fit the data equally well, and it was impossible to get parameter estimates to converge over

a reasonable range of starting conditions or parameter constraints. Presumably, this reflects differences in parameters from year to year. As another example, we did not include quantitative analysis of alternative functional forms for extinction probabilities because plots of extinctions vs. island size neatly matched the exponential function.

To obtain maximum likelihood estimates for model parameters, we separately used each of the six years of occupancy data (1972–1977) for all of the islands monitored in Pokki's study. In addition to fitting the general model, we also fitted modified versions of Eq. 4 to address a number of questions about metapopulation structure. Throughout, we use two criteria to determine the importance of processes: (1) statistical significance, as determined by likelihood ratio tests comparing nested models fitted to each year's data, and (2) consistency of patterns across years. First, we tested the importance of immigration from the mainland by comparing the fit of Eq. 4 to a model with only internal colonization:

$$J_i = \cfrac{1}{1 + \cfrac{\mu}{\left[\sum_{j=1}^{n} \hat{p}_{j,t} e^{-ad_{ij}} A_j^b\right]^2 A_i^x}}. \qquad (5)$$

Second, we tested whether extinction and colonization rates vary as functions of island location or size by fitting models with either no effect of island location (Eq. 6) or no effect of island size, other than on an island's contribution to colonization of other islands (Eq. 7):

$$J_i = \frac{1}{1 + \dfrac{\mu}{A_i^x}} \qquad (6)$$

$$J_i = \frac{1}{1 + \dfrac{\mu}{\left[\displaystyle\sum_{j=1}^{n} \hat{p}_{j,t} e^{-ad_{ij}} A_j^b\right]^2}}. \qquad (7)$$

We also compared the predictions of the incidence function model to those of the simple, nonspatial, equilibrium metapopulation model (fitted in *Simple metapopulation models: Patch heterogeneity and equilibrium dynamics*). In particular, using the incidence function model, we calculated the relative contribution of each island type (large, medium, and skerry) and the mainland to the expected number of colonizing voles in each year. The relative contribution of each island type to the pool of colonizing voles ($\hat{f}_k$) can be estimated from its mean percentage occupancy from 1972–1977 ($\bar{p}_i$), its mean weighted distance to other islands ($e^{-\alpha d_{ij}}$), and its weighted size (A_i^b), summed over all m islands in that size class. For example

$$\hat{f}_k = \sum_{i=1}^{m} \left(\bar{p}_i A_i^b \frac{1}{n} \sum_{j=1}^{n} e^{ad_{ij}}\right).$$

For the mainland, an analogous formula can be calculated

$$\hat{f}_{\text{mainland}} = \left(A_{\text{mainland}}^b \sum_{j=1}^{n} e^{-ad_{\text{mainland},j}}\right).$$

Results.—The mainland was not a significant source of colonists to the island metapopulation. Eq. 5, with internal colonization only, fitted occupancy patterns almost exactly as well as Eq. 4, with immigration from the mainland (likelihood ratio test, $\chi^2 = 3.71$, df = 6, $P > 0.7$; Table 3). Furthermore, estimates of the contribution of the mainland to colonization, based on models fitted to Eq. 4, were consistently low: at most 20% of recolonizing voles, with a best average estimate of 4%. Thus, we base all remaining statistical comparisons on Eq. 5, rather than Eq. 4.

Extinction and colonization rates varied significantly with island size and location, respectively. In all years, retaining variation in the size- and location-dependent components of the incidence function model improved model fit ($\chi^2 = 54.15$, df = 12, $P < 0.000001$; and $\chi^2 = 65.46$, df = 6, $P < 0.000001$; respectively). Fitted models predicted that occupancy would vary with patch size, in accord with Pokki's observations (Table 1, Fig. 2B).

Finally, parameter estimates based on Eq. 5 (Table 4) largely corroborate simple metapopulation model fits (Table 2) and Pokki's observation that voles are more likely to disperse from skerries than larger islands (Table 1). An island's contribution to recolonization never increased linearly with island size, as assumed in early incidence function derivations based on island biogeography (Hanski 1994*a*; i.e., $b < 1$ in all years). Half of the time, expected dispersal from small islands was greater than that from large islands ($b < 0$, the opposite trend from increasing contribution with increasing size, as assumed in all previous applications of incidence function models of which we are aware; Table 4). This trend was partially mitigated by higher mean occupancy on large islands, so that each large island was usually predicted to contribute more colonists than did each skerry (Fig. 3A). Nonetheless, in four of six years, we estimated that skerries contributed more to the total number of dispersing voles than any other island type (Fig. 3B), due to the fact that there are many more skerries than large islands in the archipelago. In spite of this, far more of the land in the archipelago is on large islands than on skerries (Fig. 1). On a per-area basis, the contribution of skerries to colonization is consistently larger than that of large islands (Fig. 3C).

In sum, these results support those of the Levins model, although predicted decline in colonist contribution with increasing island size is not quite as extreme for the incidence function model (Fig. 3B) as for the size-class Levins model (Table 2). To further explore the relationship between island size and contribution to dispersing colonists, we next use independent subpopulation-level data to predict how dispersal would vary with island size.

Dispersal patterns predicted from subpopulation data

Theoretical models of metapopulations generally assume that density per area and per capita dispersal are constant, leading to an increasing relationship between island size and net dispersal. In contrast, the Tvärminne vole metapopulation differs from ''traditional'' relationships between patch size and population dynamics in two ways: mean vole densities are slightly higher (and much more variable) on skerries than on larger islands (presumably due to higher fecundity and faster maturation; see *Study system* above), and successful per capita dispersal is higher from skerries than from larger islands (Table 1). To find out if these effects are sufficient to lead to higher net dispersal from smaller islands (which presumably is proportional to potential for providing colonists to unoccupied islands) we use subpopulation data (Table 1) to estimate the number of successful dispersers from occupied islands (D) as a function of island size (A), the rate of successful interisland dispersal per capita (d), and density (animals/area; N): In the Tvärminne vole metapopulation, density declines slightly with island area, and successful per capita dispersal declines rapidly with area. If

$$N = x_1 + x_2 A \qquad (8)$$

and

$$d = y_1 \exp(y_2 A) \qquad (9)$$

TABLE 3. Comparison of incidence function models fitted to patch occupancy data.

Model	ln(Likelihood)					
	1972	1973	1974	1975	1976	1977
Eq. 5, closed metapopulation	−40.3	−31.8	−34.1	−39.6	−33.4	−35.6
Eq. 4, immigration from mainland	−40.3	−31.8	−34.1	−39.6	−32.6	−34.5
Eq. 6, location-independent coloniza- tion, closed metapopualtion	−40.3	−37.4	−41.2	−48.6	−35.8	−38.6
Eq. 7, size-independent extinction, closed metapopulation	−45.4	−36.5	−35.9	−41.6	−46.5	−41.6

then

$$D = A(x_1 + x_2 A)[y_1 \exp(y_2 A)] \qquad (10)$$

where x_1, x_2, y_1, and y_2 are fitted parameters. We fit Eqs. 9 and 10 to summary data from Pokki (1981), summarized in Table 1. Our goal here was not to realistically model subpopulation dynamics and dispersal, but to ask whether the approximate patterns of density and dispersal are consistent with the results of incidence function modeling. In particular, we focus on the relationship between island size and its contribution to dispersing voles, the source of potential recolonists.

Using maximum likelihood and assuming binomially distributed error for each island size class, we fitted Eq. 9 to mark–recapture data for dispersing voles (row 6 in Table 1). For each size class, the available data were thus the number of voles, and the number that successfully dispersed from one island to another, for islands of each size class. Lines were fitted as functions of mean island size in each size class. (Similar results were obtained by using median sizes per class as the independent variable.) Ninety percent confidence limits (calculated using likelihood profiling; Hilborn and Mangel 1997) were used to bound the slope parameter (y_2; Table 1, Fig. 4A).

Even less data were available to estimate the relationship between vole density and island size. Pokki measured absolute vole densities on seven skerries, one large island, and no medium islands (Table 1, Fig. 4B). In other words, of eight islands for which any density data were collected, only one island differed substantially in size from the others, which is not sufficient to statistically bound the relationship between density and island size. Therefore, we attempted to estimate an approximate range of possible slope values for change in vole density with island size, based on different kinds of information Pokki (1981) collected for these eight islands. We fit Eq. 8 to three different response variables: (1) Pokki's ''ecological density'', vole density divided by vegetated area on each island, then divided by 10 to scale for 10% mean vegetative cover per island (which leads to a very steep slope), (2) vole density per total island area, rather than vegetated area (which leads to an intermediate slope), and (3) to a constant line with no slope (because these data are not sufficient to rule out the null model of no relationship between

vole density and island size). These data yield three curves, ranging from steeply negative to no relationship between vole density and island size (Fig. 4B).

Combining these relationships allows estimation of dispersal per island. This range of parameters led to maximum dispersal from medium sized islands (13, 10, and 9 dispersers per average-sized medium island; based on high, medium, and low-slope functions, respectively; Fig. 4C), on a per-island basis, and slightly higher expected dispersal from skerries (eight, four, and four dispersers per average-sized skerry; based on high, medium, and low slopes) than from large islands (two, three, and seven dispersers per average-sized large island, based on high, medium, and low slopes). Furthermore, in a typical year, the Tvärminne archipelago contained 17 skerries occupied by voles (40×0.42), 14 occupied medium islands (18×0.75), and only 10 occupied large islands (13×0.80) (see Table 1). This enhances the ecological significance of the higher number of emigrants per occupied skerry, relative to large islands.

Effects of habitat loss

While all our analyses suggest the importance of smaller islands in generating dispersers, this does not necessarily translate into metapopulation importance. Smaller islands also suffer much higher extinction rates, and thus evaluation of the net ''importance'' of smaller islands for metapopulation persistence requires further analysis. To understand these relationships, we return to the modified Levins model with three size classes of islands: skerries, medium, and large islands (Eq. 3). Using this model, we compare the expected equilibrium occupancy of the full metapopulation, with that of hypothetical metapopulations composed only of a fraction of the islands. Qualitatively similar results about the effects of habitat loss were obtained by removing islands of each type from the incidence function model (E. Crone, *unpublished data*).

Using parameters fitted to Eq. 3, the effects of removing island type i on metapopulation dynamics can be calculated by setting $f_i = 0$, and recalculating the joint equilibrium for the other two island types. Because we were not able to calculate confidence limits for f_i from the occupancy data, we also repeated these calculations using estimates of the analogous param-

TABLE 3.   Extended.

| Sum of ln(Likelihood) | Significance relative to Eq. 5 | | | Conclusion |
	df	χ^2	P	
−214.8				
−213.0	6	3.71	0.72	Mainland not a significant source of dispersers.
−241.9	12	54.15	<0.000001	Occupancy varies with location.
−247.5	6	65.46	<0.000001	Occupancy varies with island size.

eter, $\hat{f}_i$, from the incidence function models. Median dispersal values from the incidence function model were 45% from skerries, 30% from medium islands, and 25% from large islands, close to the values from the size class model (44%, 44%, and 12%, respectively), and we estimated the effects of island removals using both sets of rates. However, incidence function colonization parameters varied substantially from year to year. Therefore, we also predicted the importance of island types using source of colonist estimates from the two most extreme years. The 1974 incidence function predicted that 65% of colonizing voles came from skerries, 25% from medium islands, and 10% from large islands; and the 1972 incidence function estimated 10% came from skerries, 30% from medium islands, and 60% from large islands (Fig. 3).

Our results suggest that vole populations could not persist in systems made up of skerries alone, and that they are also unlikely to persist on large islands alone (Fig. 5). For tiny skerries, the extinction rate is too high to counterbalance even high colonization rates (Fig. 5A). For large islands, extinctions are infrequent, but persistence varies dramatically with changes in estimated disperser fraction (Fig. 5C). Only intermediate-sized islands appear to have high enough colonization to balance extinctions in isolation. Intriguingly, based on both Levin's model and median incidence function parameters, occupancy of intermediate-sized islands would be reduced about the same amount by removal of all large island subpopulations (72% of total land area in the archipelago) as by removal of all skerry subpopulations (11% of the total land area in the archipelago; Fig. 5B).

DISCUSSION

For this metapopulation, relationships between permanent and ephemeral habitats are complex. The main-

land, undoubtedly the most persistent vole population in the region, contributes little to persistence of the vole metapopulation in the archipelago, while subpopulations on marginal skerries are unlikely to persist individually, but are an important source of immigration to more permanent subpopulations on larger islands in the archipelago. Indeed, it may be the combination of persistent, low-emigration subpopulations and ephemeral, high-emigration subpopulations that allows voles to be the only mammals on outer islands in the archipelago.

Typical results from mainland–island and source–sink metapopulation models (e.g., Harrison 1991) have emphasized the importance of targeting more persistent subpopulations of endangered species for conservation, although the effects of habitat loss on subpopulation persistence depend heavily on the details of immigration, emigration, and patch quality (Gyllenberg and Hanski 1997). However, for this metapopulation, concentrating only on the largest subpopulations could be unwise. It is not clear that voles would persist on larger islands in the archipelago in the absence of recolonization from smaller islands. Similarly, it is quite unlikely that voles could persist on tiny skerries in the absence of occasional colonization from more persistent subpopulations on larger islands. This contrast with the general result of metapopulation models arises from an important difference between these models and vole dispersal behavior: the models implicitly or explicitly assume that larger and more persistent subpopulations will contribute more dispersers to the metapopulation than will smaller and more ephemeral subpopulations. In other words, there is an implicit assumption both that larger patches have larger populations and that per capita probability of dispersal is constant across patches. This is not true for the Tvär-

TABLE 4.   Parameter estimates for the closed metapopulation incidence function, fitted to occupancy patterns from 1972–1977.

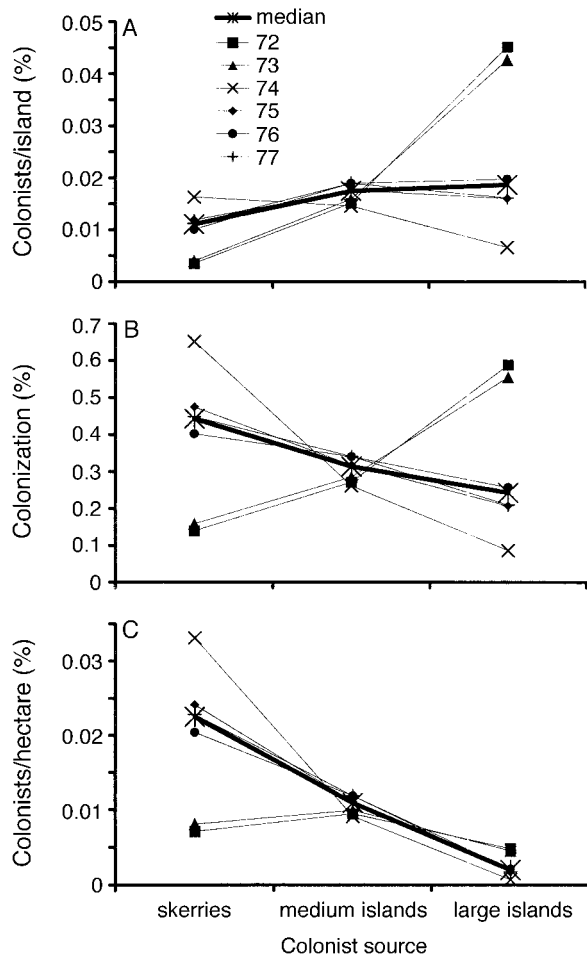| Parameter | Maximum likelihood estimates | | | | | |
	1972	1973	1974	1975	1975	1977
α	−1.06	−0.91	−2.24	−3.32	−1.88	−0.89
b	0.67	0.61	−0.48	−0.05	0.05	−0.07
μ	100	92	2.6	0.83	8.2	34
x	0.97	1.14	0.37	0.66	1.41	1.15

Fig. 3. Contribution of subpopulations on different-sized islands to colonization in the Tvärminne archipelago, calculated from separate incidence functions fitted to six years of data: (A) contribution to colonization per island, by size class; (B) percentage of total colonists provided by all islands in each size class; (C) contribution to colonization per land area (ha), by size class.

minne vole metapopulation, with a substantially more complex relationship between patch size and dispersal.

What are the relationships between individual behavior, within-subpopulation dynamics, and metapopulation processes? On larger islands, overcrowding leads to dispersal from optimal habitat to suboptimal habitat; there is even limited evidence for superannual population cycles in response to crowding (Pokki 1981). On smaller skerries, there are actually higher vole densities, suggesting higher quality habitat. However, there is simply no suboptimal habitat to which voles can disperse when resources (either food or space) are exhausted. Given these observations, and the almost complete lack of vole immigrants to the islands from the mainland, it is tempting to speculate that dispersal is a risky behavior which voles only undertake in dire circumstances. This highlights another difference between vole metapopulation dynamics and
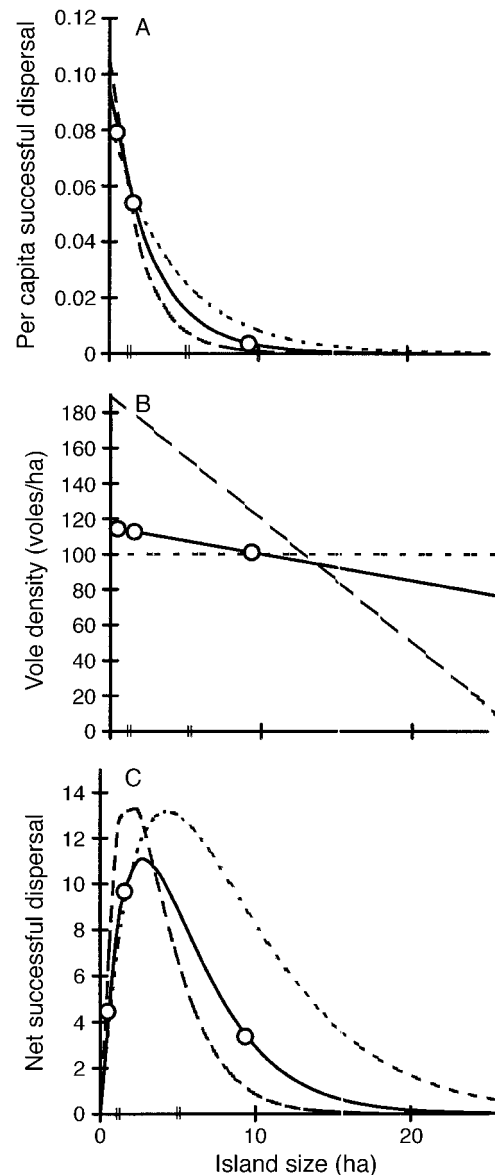

Fig. 4. Relationships between island size, vole density, emigration rates, and net emigration from islands of different size: (A) per capita emigration vs. island size, with parameters in Eq. 9 estimated as $y_1 = 0.106, 0.094, 0.082$ and $y_2 = -0.5$, $-0.35, -0.25$ for upper 90% confidence limit for slope (y_2; high slope), maximum likelihood parameter estimates (medium slope), and lower 90% limit (low slope), respectively; (B) density vs. island size, with parameters in Eq. 8 set to $x_1 = 190, 115, 100$ and $x_2 = -7, -1.5, 0$ for ecological density (high slope), absolute density (medium slope), and no slope (low slope) models; (C) net emigration per island vs. island size, calculated using Eq. 10 and high, medium, and low functions described in A and B. For all three figures, thick lines show high slope parameters, medium lines show medium slope parameters, and thin lines show low slope parameters. Double lines on the horizontal axis demarcate the three island size classes: <1 ha skerries, 1–5 ha medium islands, and >5 ha large islands. Circles indicate mean size in each island size class.
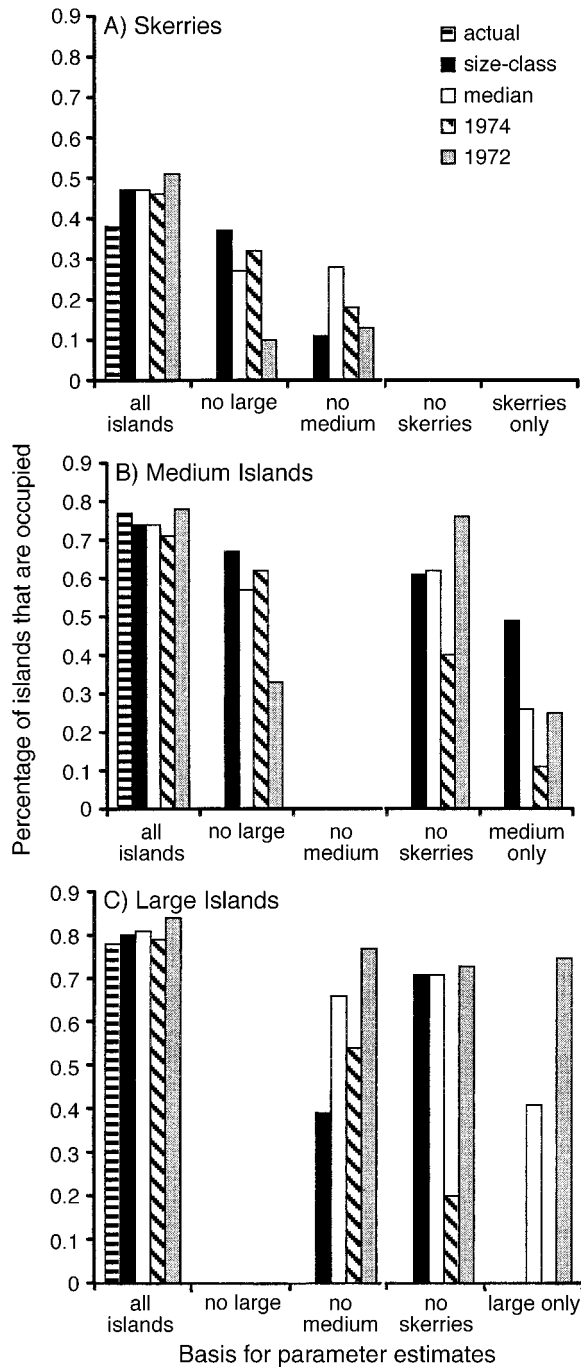
FIG. 5. Expected changes in equilibrium occupancy of islands in the Tvärminne archipelago, with elimination of islands of different sizes. Graphs show actual and predicted changes in percentage occupancy for (A) skerries, (B) medium islands, and (C) large islands. Separate results are plotted for predictions based on four different estimates of the percentage of colonists coming from different island types: parameters fitted to the size class model, median incidence function parameters, and incidence functions fitted to the two most extreme years (1972 and 1974).

metapopulation models. Typically, models assume that there is either no correlation or a negative relationship between a subpopulation's extinction probability and its production of emigrants, either in time or in space. This might be true for some species, but, given bad conditions and mobile animals, in many cases animals will move rather than passively die. Although less complete, several other recent studies of vole populations document higher population densities and/or higher emigration rates from smaller patches, or record higher overall density of voles on fragmented than unfragmented landscapes (Diffendorfer et al. 1995, Johannesen and Ims 1996, Wolff et al. 1997, Dooley and Bowers 1998).

The Tvärminne vole metapopulation is an interesting variant of the typical assumptions of metapopulation theory, in that a substantial fraction of extinctions are caused by deteriorating environmental conditions, rather than demographic stochasticity or sudden catastrophes. However, many other natural examples of published metapopulations include at least some component of slow changes in environmental quality as a cause of extinction, in addition to sudden extinctions (e.g., vegetation succession [Menges 1990] and drying of ephemeral ponds [Sjorgen-Gulve and Ray 1996]). The assumption that declining conditions in a habitat island will not increase emigration comes from the abstraction of each subpopulation in a metapopulation as a simple "on" or "off" entity. Changes in dispersal rates with population densities and habitat quality are widely studied for many taxa (see Turchin 1998 and references therein). Incorporation of this interplay between individual behavior and population dynamics into metapopulation theory may be essential for improvement of our understanding of spatial ecology.

More generally, there is every reason to believe that, even in the absence of density-driven habitat quality changes, per capita emigration may be negatively related to patch size and positively related to extinction rate. Because ours is the first study that uses incidence function models capable of showing higher colonization from smaller patches, it is not surprising that others have not found that smaller patches are more important than larger ones for metapopulation persistence. In fact, classical theoretical models of minimum patch size based on random movement (Skellam 1951, Okubo 1984; see also Holmes et al. 1994)—which have not been explicitly linked with metapopulation models— prove this expectation clearly. With random movement, more dispersers leave smaller patches, and this, in turn, fuels higher extinction rates in smaller patches. While these influences may not always lead to smaller subpopulations being of greater importance in metapopulations, they point to the possibility that the Tvärminne vole metapopulation is not unique in this regard. Indeed, in a very different metapopulation, smaller host plant patches were much important than continuous habitat for metapopulation persistence in a geometrid

moth (Doak 2000*a, b*; note that P. Doak is not a co-author of this study). Several other studies of spatially structured butterfly populations (Hill et al. 1996, Sutcliffe and Thomas 1997) demonstrate higher per capita emigration from smaller habitat patches, though these studies have not explicitly quantified effects of patch size on metapopulation persistence.

A second goal of our analyses was to test the ability of both very simple and rather complex metapopulation models to predict behavior of a well-understood metapopulation. In our analyses, many incidence function parameters differed dramatically from year to year; with only one or two years of data one could reach extremely different conclusions than we did. Clearly, based on our results, it would be risky to infer long-term dynamics or to base management strategies on straightforward application of either incidence function models or Levins' metapopulation models. On the other hand, from the set of incidence function models, we detected a clear signal that the mainland was not a significant source of colonists in the archipelago, and we were able to quantify (or at least bound) dispersal patterns among habitat patches. Furthermore, while the subpopulation and individual-level data we used allowed us to better interpret the metapopulation model results, they did not prove necessary to correct any results of the models. Thus, while the dangers of misinterpretation are considerable, we believe that these models can improve our understanding of long-term metapopulation processes, when used flexibly across a range of ecological assumptions.

In summary, our reanalysis of this vole metapopulation reaffirms the utility of the basic metapopulation approach, while cautioning that often too much is assumed about the mechanisms and patterns generating extinction/colonization dynamics. Because of the wealth of data amassed by Pokki for this system we have been able to test many assumptions about metapopulation structure that are usually inaccessible. Depending on the application, there may be little reason to make metapopulation approaches highly detail oriented and overly complicated. However, most metapopulation-like populations may need careful consideration of how underlying ecological and behavioral mechanisms can shape the rules by which metapopulation dynamics play.

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