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A USEFUL ROLE FOR THEORY IN CONSERVATION[1]

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Nothing's for certain, it could always go wrong
—The Grateful Dead

INTRODUCTION

Conservation biology has frequently been designated a "crisis discipline" (Soulé 1985, Maguire 1991). This moniker refers both to the urgency of the issues that conservation biologists seek to address and to the fact that during crises there is rarely time to assess a situation carefully before one must act. Indeed, the paucity of data available for most endangered species, communities, and ecosystems often forces biologists and policy makers to make management decisions without any quantitative information. Further, this lack of data may be insoluble: many management decisions have to be made hurriedly, and rarity itself precludes the quick or easy collection of data on threatened species or communities.

Conservation biologists have compensated for this pandemic lack of data by relying heavily upon theoretical techniques and empirical generalizations. These include simulation and analytical models for specific species and communities, the use of generalized principles derived from island biogeography concerning habitat structure and species diversity, and genetic rules governing the loss of heterozygosity and the effects of inbreeding depression. However, the use of theory in the formulation of important, concrete decisions about real species and communities has come under increasing attack. Various commentators have voiced concerns that theoretical generalizations are often too weak to be usefully predictive (B. Taylor 1991, Gibbons 1992, Estes et al., *in press*), that many valid generalizations are self-obvious platitudes (Gilpin 1991, Soberon 1992), that models are often both too simplistic and effectively untestable (Shaffer and Samson 1985, Soulé 1987, Simberloff 1988), and that many theoretical generalizations have reached the status of dogma, inhibiting scientific discussion of conservation issues and ignoring the di-

versity of ecological and historic processes affecting specific systems (Simberloff and Abele 1976, Lande 1988a).

We will highlight these concerns about the role of theory in conservation by discussing two of the ecological theories that have proven the most influential in conservation biology: the theory of island biogeography and the theory of metapopulation dynamics. We find that while these and other theories have much to offer, and indeed, must be used to address many conservation issues, both of these theoretical constructs have been overgeneralized and are often irrelevant to the formulation of practical conservation plans. Following our examination of these two case studies, we assess the general problems faced in applying theory to conservation problems and conclude with suggestions on how to improve the contributions of theory to conservation planning.

ISLAND BIOGEOGRAPHY MODELS

Conservation and traditional island biogeography theory

In their equilibrium theory of island biogeography, MacArthur and Wilson (1967) proposed that the number of species inhabiting an island results from a dynamic equilibrium between immigrations and extinctions. By the early 1970s a distinction had been made between ancient oceanic islands that support this equilibrium number of species and recently isolated landbridge islands on which species number is above the extinction–colonization equilibrium. On these landbridge islands, biogeographers hypothesized that extinction exceeds colonization, resulting in steadily decreasing numbers of species (Brown 1971, Diamond 1972). The implications of these extinction-driven processes were not lost on conservation biologists, who quickly made use of the analogy between landbridge islands and newly created habitat remnants, such as parks surrounded by development (Diamond 1972, Terborgh 1974). By the late 1970s, results from island biogeography theory were widely applied in conservation decision making, especially to the design of na-

ture reserves (Simberloff 1976; reviews by Boecklen and Gotelli 1984, Zimmerman and Bierregaard 1986).

However, this happy marriage of ecological theory and applied conservation did not last long. Since the early 1980s the application of island biogeography theory has been roundly criticized on statistical and ecological grounds. Although it is accepted that, all other things being equal, the number of species a nature reserve supports is an increasing function of the reserve area, more specific predictions have been opened to considerable debate. In particular, the claim that species–area curves can be used to predict the number of species persisting in a reserve of a given size has been attacked for several reasons: the transformations of the regression models are often improperly chosen and have low explanatory power under the best of conditions, outliers are not properly considered, there is widespread difficulty in accurately measuring the independent variable (area), and inferences have often been made outside the range of values from which parameters have been estimated (Connor and McCoy 1979, Martin 1981, Boecklen and Gotelli 1984, Loehle 1990, B. Taylor 1991).

While proper sampling design and analysis can alleviate many of these statistical problems, there are also deeper ecological problems in applying the predictions from species–area curves to conservation issues. Perhaps most important is an assumption that is fundamental to the application of island biogeography to conservation: that the units of conservation interest (we will call them habitat remnants) are analogous to landbridge islands. While MacArthur and Wilson (1967) and MacArthur (1972) repeatedly described "habitat patches" such as farmer's woodlots and recent fire burns as "islands," they were also careful to differentiate them from oceanic islands by saying that the latter "are separated by a vacuum insofar as land birds or insects are concerned, whereas mainland islands are separated by other habitats filled with birds and insects" (MacArthur 1972:105). Unfortunately, subsequent applications of island biogeography have presumed a greater degree of isolation for habitat remnants than the data support; depending on the matrix surrounding a particular remnant, some species may not be isolated at all, while others may, in fact, be trapped on what is for them the equivalent of an oceanic island (Margules et al. 1982, McCoy 1982, Janzen 1983, Mader 1984; but see Newmark 1985, 1987).

Related to the problem of species-specific isolation is another rather obvious, but often unheeded, concern: "all other things" are rarely equal for islands (or reserves) of different sizes or in different locations (Simberloff and Abele 1982, Lahti and Ranta 1985, Zimmerman and Bierregaard 1986). While these differences can be controlled in experiments, in the "real world" they will often make species–area relationships too weak to be of any utility in land use planning.

A final concern regarding the use of island biogeography is that while the theory may make strong and accurate predictions about species numbers and extinction rates, it has little to say about the identity of the species going extinct or the sequences of extinctions, an important deficiency when addressing the protection of particular species (Simberloff and Abele 1982, Margules et al. 1982, Lahti and Ranta 1985). Responding to this criticism, some authors have advanced techniques such as incidence functions to predict the order of extinctions for particular species (Diamond 1975, Gilpin and Diamond 1981). However, in a review of the use of incidence functions for conservation, B. Taylor (1991) observes that while the technique's predictive power is high for the numbers of species on habitat remnants, it is weak for the identities of the species persisting on small remnants, due to the effects of body size, abundance, and temporal variations in population size on extinction probabilities (see also Soulé et al. 1988). Thus, it is not clear that incidence functions will aid in the use of biogeographic data for conservation planning.

As a result of the controversies and criticisms discussed above, most current applications of island models in conservation focus on hypothesis testing to illuminate the general trends and mechanisms underlying population dynamics on habitat remnants (e.g., Newmark 1987, Lomolino et al. 1989, Bolger et al. 1991). In addition, biogeographic studies in conservation are increasingly using a technique that makes explicit the identities of species on remnants: nested subset analysis.

Nested subset analysis

First introduced to conservation biology by Patterson and Atmar (1986), nested subset analysis expands upon the species–area curve approach by keeping track of not only the numbers but also the identities of the species occurring on each island within an archipelago. Nested subset analyses then test for patterns between species identities and the numbers of species occurring on different islands. In particular, these analyses ask whether the species occurring on species-poor islands are merely subsets of the species living on biotically richer islands. To the extent that such nestedness is generated by extinctions (e.g., "faunal relaxation" on landbridge islands), a nested pattern implies that a predictable or deterministic sequence of extinctions has occurred through time on each island (Patterson 1987, Cutler 1991), and thus that some species are more at risk from future extinctions than are others. Cutler (1991) demonstrated the value of nested subset analysis by observing that the order of extinctions as re-

vealed by nested subsets can often be more predictable than the rate of extinctions, based on traditional species–area curves.

It would obviously be useful if the predictable extinction sequences that nested subset analyses identified on static islands could be linked to species losses that will occur as "island" sizes decrease due to habitat loss (Patterson 1987, Cutler 1991, McDonald and Brown 1992). However, there are dangers in assuming that a nested pattern implies that a predictable extinction sequence will result from shrinking remnant size. The nested subset pattern itself does not even consider island sizes, and thus it is quite possible to have a nested subset and no significant species–area relationship, or visa versa. Thus, while nested subset analysis might be used to identify which species are most at risk of extinction, it cannot readily be used to predict extinction sequences resulting from habitat loss, or the total number of species that will persist on habitat remnants of different sizes.

While, as a statistical technique, nested subset analysis is an obvious improvement over species–area curves, and requires essentially no more information, there are still serious problems that will hamper its applications in conservation biology. Perhaps most importantly, as with island biogeography, the utility of this new technique will depend on the extent to which habitat remnants are analogous to landbridge islands. This sensitivity results because species extinctions and colonizations will be idiosyncratically affected by nuances of the biotic matrix surrounding habitat remnants (Laurance 1991), undermining the basic assumption that "Because preserves are progressively made insular by outside habitat disturbances, the derivation of their biotas is closely analogous to those of landbridge islands . . ." (Patterson 1987:332).

Related to the basic difficulties posed by the appropriateness of the island analogy is the need to decide which species to include in the analysis at all. While it is obvious that in oceanic settings terns or albatrosses should not be considered in an analysis of extinction sequences for landbirds, the lack of an oceanic "vacuum" (sensu MacArthur 1972) around mainland habitat remnants clouds the issue. The usual approach for both species–area and nested subset applications is to include only "specialists" to the habitat type present in the remnant. But, as Mader (1984) showed for beetles and spiders, remnants can reach such small sizes that the number of "non-characteristic" species can actually be greater than the number of species characteristic of the formerly continuous natural habitat. In this case, a focus only on "specialists" will miss many of the important dynamics in species abundances and interactions (McCoy 1982).

The problem of predicting extinction sequence is made more complex by sampling error. Two difficulties must be overcome before drawing valid conclusions regarding extinction sequence based on nested subset analysis (see Cutler 1991). First, sampling (e.g., mammal trapping, bird counts, etc.) may be biased by species-specific capture probabilities such that rare, localized, or difficult-to-capture species may show up randomly on remnants. Such a species would tend to appear as an "unexpected presence" (Cutler 1991), or outlier. This would not only cause an artifactual deviation from nestedness, it would also improperly indicate an artificially high extinction risk for that species. Related to this potential artifact are "sampling effects" (Bolger et al. 1991). By chance alone, certain species may actually be absent from smaller remnants. While this is the stuff of conservation biology, i.e., what types or sizes of reserves must be saved to insure that we don't by chance miss some species, it merely results in noise in the nested pattern, thereby decreasing the strength of the patterns that the analysis seeks to find. Although the technique may well identify suites of species that require special attention, i.e., low density, patchily distributed, endemic, or otherwise extinction-prone species, the ranking of expected extinction sequence, and therefore conservation priorities, will almost certainly be of dubious accuracy.

Finally, we recommend a cautious approach to interpreting the statistical significance of nested subsets. At present, deviation from nestedness is assessed by comparison of the actual archipelago with Monte Carlo simulations (Patterson and Atmar 1986, Cutler 1991). Under certain conditions, the power of this test (i.e., ability to detect a nested pattern) is very low (Mills 1993). Furthermore, a "significantly nested" archipelago may still have large deviations from nestedness (as discussed by Patterson 1987, Cutler 1991), so that even a strongly nested archipelago may have many species that cannot be correctly "ranked" in terms of, for example, extinction susceptibility.

To demonstrate some of the potential pitfalls of using island biogeography and nested subset analyses to predict extinctions on shrinking habitat remnants, we provide a hypothetical example in Fig. 1. For these nine hypothetical species occurring on 10 habitat remnants there is a significant species–area relationship ($r^2 = 0.57, P = .01$) and the species are significantly nested in distribution (Cutler's RANDOM1, $z = -2.7, P = .004$). However, the ranking of remnants by size (A to J corresponding to largest to smallest, Fig. 1a) differs considerably from ranking by species richness (Fig. 1b). Thus, smaller remnants do not necessarily have the fewest species, as is often assumed on the basis of simultaneously significant species–area and nested subset relationships. Consequently, we cannot assume that the species that are on the fewest remnants are confined
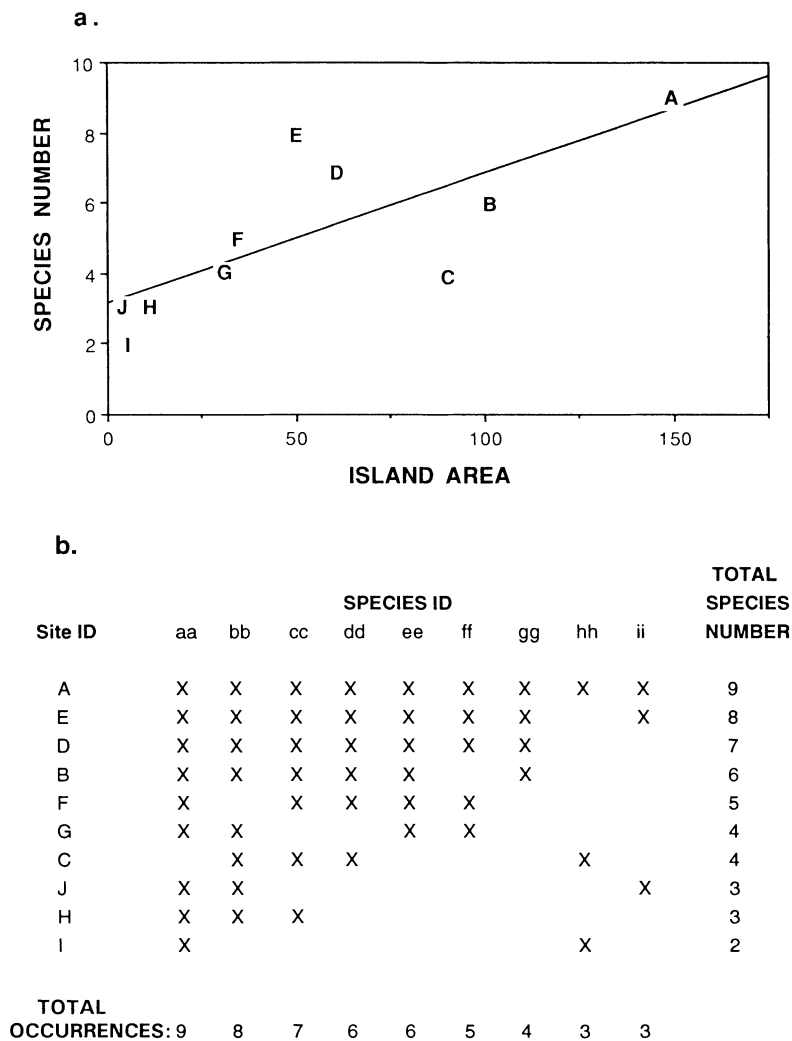
a.

b.

Site ID	aa	bb	cc	dd	ee	ff	gg	hh	ii	TOTAL SPECIES NUMBER
A	X	X	X	X	X	X	X	X	X	9
E	X	X	X	X	X	X	X		X	8
D	X	X	X	X	X	X	X			7
B	X	X	X	X	X		X			6
F	X		X	X	X	X				5
G	X	X			X	X				4
C		X	X	X				X		4
J	X	X							X	3
H	X	X	X							3
I	X							X		2
TOTAL OCCURRENCES:	9	8	7	6	6	5	4	3	3	

FIG. 1. Biogeographic analysis of a hypothetical archipelago of 10 habitat remnants (presumed "islands") and nine species. Single capital letters designate the remnants, while double lowercase letters identify the species. (a) Data plotted as an untransformed species–area regression. (b) Data in format for nested subset analysis, with " × " indicating species present on that remnant. Both the species–area curve and the nested subset analysis are statistically significant, but the species are distributed such that equating lack of occurrence on small remnants with extinction susceptibility would be misleading.

to the largest remnants; these species may have colonized from the surrounding matrix, or possibly require habitat components found randomly on remnants. In this fictional but biologically plausible archipelago, it is obvious that nested subset techniques can only support statements regarding predictability of species lost as we go from the more species-rich to species-poor remnants; it does not support either the general statement that species are lost in a predictable sequence from large to small remnants, nor specific claims regarding the species on the fewest remnants. For example, we could not say generically that "species hh and ii are most in danger of extinction due to shrinking

remnant size." As we hope this example illustrates, neither nested subset analysis nor island biogeography theory provide strong enough inferences to obviate the need for species-specific ecological information when considering conservation planning (see also Patterson 1987, Cutler 1991, MacDonald and Brown 1992).

METAPOPULATION DYNAMICS

We do not wish to thoroughly review the history or meaning of "metapopulation" or "metapopulation dynamics" (see Hanski and Gilpin 1991 for an excellent review). Therefore, we simply note that as originally

conceived and modeled by Levins (1969) and as usually modeled and used now, a metapopulation refers to a collection of populations, each existing on a patch of suitable habitat that is separated from other habitat patches by unsuitable terrain. These separate populations are envisioned as undergoing repeated extinctions and recolonizations. Thus, although each population has its own, relatively independent dynamics, the long-term persistence and stability of the metapopulation arise from a balance between population extinctions and the founding of new populations through relatively infrequent dispersal events. Indeed, the "turnover" of local populations has been called the "hallmark of genuine metapopulation dynamics" (Hanski and Gilpin 1991).

Although the above definition of a metapopulation has recently been expanded to include many types of spatially distributed populations (Hanski and Gilpin 1991), this "classic" idea of a metapopulation is still the one envisioned by most ecologists and conservation biologists. Importantly, this classic conceptualization of metapopulation dynamics arose almost entirely from modeling, starting with Levins' theoretical work (Levins 1969). Similarly, much of the subsequent work on metapopulations, and essentially all of the most influential papers on the subject, have been modeling efforts (e.g., Lande 1987, Harrison and Quinn 1989), rather than field studies. A recent symposium volume devoted to metapopulation studies includes 10 primarily theoretical papers and only 3 contributions that were largely empirical (plus 5 reviews, Gilpin and Hanski 1991). Clearly, the development of metapopulation ideas has been for the most part a theoretical endeavor.

Over the past 5 yr or so, the ideas of metapopulation behavior and dynamics have rapidly gained influence in the conservation literature. Hanski (1989) states that ". . . the theory of metapopulation dynamics is replacing the equilibrium theory of island biogeography as the population ecology paradigm in conservation biology," while Hanski and Gilpin (1991) observe that "Metapopulation ideas have recently become the vogue in conservation biology . . ." this interest in metapopulations has translated both into studies of specific species (e.g., Lande 1988b, Thomas et al. 1990, Kindvall and Ahlen 1992, Lamberson et al. 1992) and into a belief in the general importance of metapopulation dynamics for conservation biology (Gilpin 1987, Hanski 1989). For example, in discussing small, short-lived species with high habitat specificity, Murphy et al. (1990) state that "Population viability analyses for these species . . . must focus on the environmental factors and metapopulation characteristics that determine population persistence." Given the eminence of metapopulation ideas in current conservation biology, it is important to answer three questions: Is the classic conception of a metapopulation commonly accurate or applicable for past or current populations? Can we, in practice, determine the importance of metapopulation dynamics for real populations? and, What is the desirability of attempting to create metapopulations of rare species?

Are metapopulations common?

Several recent reviews of empirical work have called into question the prevalence of classic metapopulations (Harrison 1991, A. D. Taylor 1990, 1991). These authors note that there are many ways for a population to exist in a patchy landscape that do not involve local population turnovers due to extinctions and recolonizations, or in which such turnover occurs, but is unimportant. In particular, Harrison notes that patchily distributed populations commonly show three patterns that are qualitatively different from the classic metapopulation model. First, if one or more habitat patches are "big," while other patches are "small," then the big populations on the big patches are unlikely to suffer extinctions often, or at all, while the small populations may undergo frequent extinctions and recolonizations (e.g., Bengtsson 1991). In this "core–satellite" case, the internal dynamics of the large islands will determine the population dynamics and viability of the entire species, with the extinction–colonization events on the smaller patches being essentially unimportant.

A real-life example of this pattern may be shown by the threatened Bay Checkerspot butterfly, *Euphydryas editha bayensis*. Murphy et al. (1990) assume that metapopulation dynamics are important for the species, maintaining that their proposed population viability analysis plan for the species "exemplifies the environment–metapopulation approach." In contrast, Harrison (1989, 1991) has argued that this subspecies lives in a core–satellite pattern, with one large, and essentially immortal, population, and several small ones, whose frequent extinctions and colonizations are largely irrelevant for the overall population viability of the butterfly. It is important to note, however, that if a core population ever suffers extinction, even the tiniest satellite populations might be crucial for the metapopulation's long-term persistence. The difficulty in estimating the probabilities of such "catastrophes" thus suggests caution in dismissing the importance of small populations.

A second situation in which metapopulation phenomena are unlikely to be important is Harrison's "patchy population" scenario. In this case, successful dispersal events are frequent, too frequent to allow for extinctions. Thus, individual patches support parts of a single population, rather than individual populations. In an example of this scenario, Stacey and Taper (1992) found that a small and seemingly isolated population

of Acorn Woodpeckers was not maintained by classic metapopulation dynamics. Rather, immigration rates were high enough to account for almost half of the total adult recruitment. As Stacey and Taper point out, even though this woodpecker population is physically isolated, it is still "in a demographic sense . . . part of, and intimately connected to, other populations." As with island biogeography models, we see that "isolation" is a pivotal variable; in this case, movement and spatial arrangement are important, but the extinction–recolonization processes envisioned by metapopulation models are not. As Harrison (1989, 1991) points out, this pattern is the one expected for most species that evolved to exploit patchy habitats.

A last class of population dynamics is that of a set of declining populations, in which extinctions outstrip recolonizations. While it is obvious conceptually that these declining populations are not stable metapopulations, it may be extremely difficult to distinguish slow decline from stability in the field (Harrison 1991). This is especially true if changing conditions (often anthropogenic) convert stable metapopulations into declining ones.

Finally, we note that even when field studies do show clear metapopulation dynamics it is not always clear how widespread these dynamics are for the species being studied, since many of the best examples of metapopulations are for species in unusual circumstances. For example, many studies of the metapopulation dynamics of typically mainland mammals have been conducted on sets of small islands (e.g., Pokki 1981, Peltonen and Hanski 1991). Similarly, Sjogren's (1991) study of the metapopulation dynamics of a frog was conducted at the edge of the species geographic range. Overall, the weak evidence that classic metapopulations are common in nature should make conservation biologists cautious about assuming that metapopulation dynamics are important for the population viability of rare and endangered species.

Can we determine when metapopulation dynamics are important?

While there are clearly myriad ways in which populations can deviate from the assumptions, and therefore dynamics, of a classic metapopulation, it will often be difficult or impossible to distinguish between these alternatives, and thus to assess the importance of metapopulation dynamics. Levins' original (1969) models and simple derivations of them (Gotelli 1991, Hanski and Gilpin 1991) have minimal data requirements, due to a variety of simplifying assumptions: all patches are the same size; patches are randomly distributed or are all equidistant; patch population sizes do not affect extinction or emigration probabilities. Yet even for these simple models, Gotelli (1991) has shown that

very different behaviors arise with varying assumptions about the dependence of patch extinction and colonization on population number (i.e., patch "density dependence"), assumptions that will be extremely difficult to distinguish with field data.

Perhaps a more serious difficulty in assessing metapopulation dynamics arises due to the detailed data that are needed to parameterize most metapopulation models and to assess the sensitivity of a model's output to its parameter values (Gilpin 1987, Hanski 1991). While Levins' model is quite simple, metapopulation models for particular species are typically much more complex, requiring many more assumptions and parameter estimates. In particular, three distinct classes of information are needed to understand and model metapopulation dynamics accurately. First, all the data required for a simple demographic model, including estimates of the means and variances of all vital rates, are necessary to understand within-population dynamics and the extinction and emigration rates that arise from them. Even this basic information is usually unavailable for rare species. In addition to within-population estimates of vital rates, estimates of the degree to which variations in these rates are spatially and temporally correlated between populations is essential for an understanding of the extinction–recolonization process (Harrison and Quinn 1989). However, few ecological studies of any species occur on either the temporal or spatial scales necessary to obtain such data (Kareiva and Anderson 1988, Doak et al. 1992), and it will be especially difficult and costly to collect this information for the rare species of most interest to conservationists. Lastly, data on dispersal distance and success are necessary to understand a metapopulation's behavior. Like information on spatiotemporal variation in vital rates, long-distance dispersal information is notoriously hard to obtain (Chepko-Sade and Halpin 1987, Harrison 1992) or model accurately (Buechner 1987, Rogers and Klenner 1990).

Thus, while metapopulation models are not untestable in theory, they will often prove to be so in practice. Further, metapopulation models using poor or incomplete data on dispersal or spatiotemporal correlations can easily yield predictions that will differ qualitatively from actual behavior. Of particular worry is that modeling based on poor data could easily predict stability when a nonequilibrium condition actually exists. Importantly, this problem is not restricted to classic metapopulations, but is also relevant to many other spatial models, which are unavoidably data hungry simply due to their complexity.

Should we try to create metapopulations?

Much of the enthusiasm for metapopulation ideas has stemmed from a desire to understand extinction

probabilities and formulate management decisions for rare species already emplaced on habitat patches. However, conservationists have also suggested the creation of metapopulations for endangered species as a way to maintain populations on increasingly fragmented habitat patches. The most celebrated example of this strategy is that of the Interagency Spotted Owl Scientific Committee (the ISC, Thomas et al. 1990). The ISC's plan to maintain Spotted Owl populations relies on the creation of large areas of suitable forest habitat. These areas need to be of sufficient size and proximity so that losses of owls from forest remnants will be infrequent enough, and dispersal between remnants will be likely enough, that owl numbers will be stable on the entire archipelago of forest fragments.

While the ISC plan represents one of the most comprehensive and scientifically based management plans for any endangered species (see Murphy and Noon 1992, Harrison et al., *in press* for overviews of the ISC plan), the controversy over the safety of the plan highlights the uncertainties involved when attempting to predict the workings of a metapopulation. Data for the Spotted Owl are superb in comparison to those available for most rare species (or even many common ones—the chair of the ISC, Jack Ward Thomas, has quipped that we know more about Northern Spotted Owls than we know about mule deer). In spite of this rich base of information, models for owl metapopulations must assume a great deal about owl biology, especially juvenile dispersal behavior and mortality (Thomas et al. 1990, McKelvey et al. 1992). These problems have made assessments of the models', and hence the plan's, "safety" difficult to defend (Dwyer 1992, Harrison et al., *in press*), a crucial problem when trying to implement a management strategy. We suspect that similar concerns will, and perhaps should, arise with other applications of spatial modeling to particular species and ecological communities; the near impossibility of adequately parameterizing the models makes their conclusions highly suspect. This does not mean that the models are worthless, only that they should be used cautiously when evaluating the safety of long-term or irreversible land-use decisions.

The utility of metapopulation models in conservation

Although we question the generality of metapopulation dynamics and the applicability of metapopulation models to specific problems in conservation, the theory has had positive effects in conservation research. In particular, interest in metapopulation dynamics has prompted renewed research concerning dispersal capabilities that is extremely valuable in understanding population structure. Metapopulation models investigating the effects of correlations in ex-

tinction risks and dispersal probabilities have also led to greater concern about these phenomena among field researchers. In these cases, the utility of metapopulation models has been to heighten awareness of risks, rather than to quantitatively evaluate these risks. A specific application of this type is Lande's model for the Northern Spotted Owl (Lande 1988b). Although Lande modeled a specific species, the point of his analysis was to document the probability that a particular type of ecological process (reduced juvenile dispersal success resulting from increasingly fragmented habitat) could lead to the extinction of the species. Even though the model could not be accurate enough to yield exact quantitative predictions, it forced policy makers to seriously consider a previously overlooked threat.

The most recent advances in metapopulation modeling emphasize spatially explicit, often GIS-based (Geographical Information System) population simulations. Because these simulations can include extremely detailed spatial structure, they have been advocated as more accurate and useful than earlier, less "realistic" models (e.g., Pulliam et al. 1992). However, we are not sanguine about the general utility of this approach; all the problems associated with parameter estimation and model complexity are magnified for spatially explicit models, in which one must parameterize, for example, not just immigration rates, but also the nuances of disperser behavior (Pulliam et al. 1992). While GIS-based models for extremely well-studied species, such as the Spotted Owl, have already proven their utility (McKelvey et al. 1992), we fear that the construction of such detailed simulations will be counterproductive for many species, giving the illusion of exactitude in the absence of hard information.

To emphasize the need for good data when developing or interpreting the results of complicated spatial models, we show some results from a spatially explicit simulation model designed to examine the effects of habitat arrangement on disperser success. In the model, dispersing animals move randomly in a landscape containing "archipelagos" of habitat patches. Within the archipelago, these patches are either arranged completely randomly or are randomly clustered into either 1, 5, or 10 groups (with randomly placed outliers; see Doak et al. 1992 for details). Four replicate landscapes were created for each arrangement. For each landscape, one disperser is released from each of the 625 islands and allowed to move until finding a new island; dispersers can detect patches that they are near to, and hence do not have to bump into a patch to find it. Dispersers move a constant distance each "day" of the simulation, and each day the direction they move is randomly determined.

We can use this model to examine two measures of disperser performance that will often, in practice, be
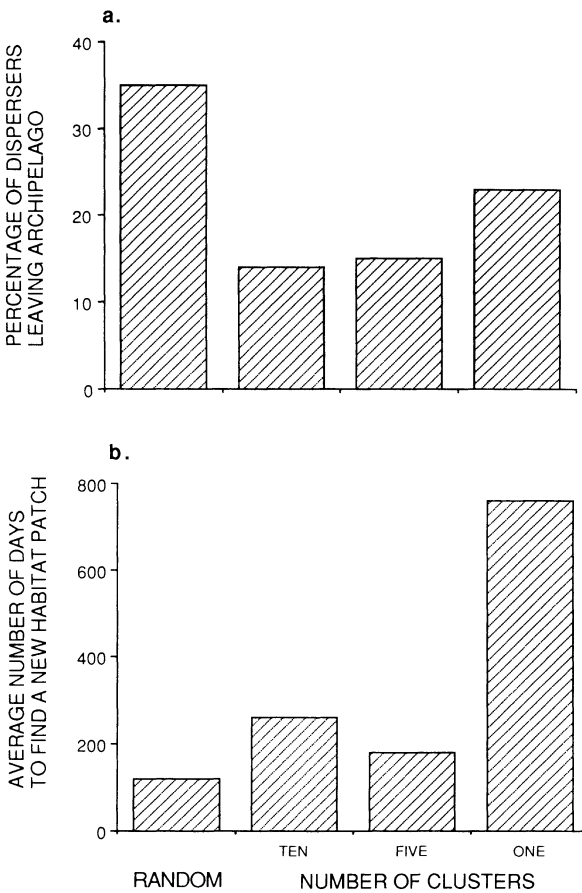
a.

b.

FIG. 2. Results from a spatially explicit simulation model of dispersing animals searching for habitat patches. Patches are arranged either randomly, or with high probabilities of occurring in either 1, 5, or 10 clusters within the landscape. The least spatially clustered landscapes are the random arrangements; the most clustered are the ones with a single cluster of islands. (a) The fraction of dispersers that ever reached the edges of the area containing habitat patches (the archipelago boundary). (b) The mean duration of dispersal for animals that never reached the archipelago boundaries. See Doak et al. (1992) for details of simulation structure and results.

biologically significant: (1) what fraction of the dispersers reaches the edge of the archipelago area, and hence venture out of the region in which there is any hope of finding a new habitat patch, and (2) for those animals that do not ever leave the vicinity of the archipelago, how long does it take to find a new habitat patch? The fraction of animals leaving the archipelago is important if mortality risks are low for dispersers moving within the archipelago area, but much higher for those that leave the vicinity of the archipelago (e.g., if the matrix between the habitat islands is second-growth forest but housing subdivisions surround the entire archipelago). However, movement between patches within the archipelago might also be dangerous, with a high probability of death each day for dispersing animals. In this case, the mean dispersal time for animals staying within the archipelago will also be an important determinant of disperser success and hence metapopulation dynamics.

From Fig. 2a it is clear that if one was mostly concerned with the loss of dispersers from the archipelago region, then an intermediate amount of habitat clustering (5 or 10 clusters) would be most advantageous. In contrast, if one wanted to minimize the average dispersal time of dispersers that stayed within the archipelago, then the best landscape design would be a random arrangement of habitat patches (Fig. 2b). Never, by the two criteria we consider here, is the most tightly clustered landscape (a single cluster of patches) the best, although a change in the movement rules could easily change this conclusion. Our point here is not to produce a generalization about optimal landscape arrangement, but rather to illustrate just how difficult it is to say anything with the model without knowing the nuances of mortality probabilities and movement behaviors for a particular species, nuances that are virtually never known.

Given the data limitations usually faced by conservation biologists, the most useful approach to the modeling of spatially structured populations may often be to consider only the largest of spatial scales or phenomena. For example, Wootton and Bell (1992) evaluate the "metapopulation" of Peregrine Falcons in California by dividing the entire state into just two subpopulations. By choosing such a large scale for their model they avoid the need for detailed, and unavailable, data on dispersal behavior or spatiotemporal variations in demography. Instead, they need only estimate the fraction of juvenile falcons moving from one-half of the state to the other, and their model thus allows them to reach useful and robust results regarding population health and species management, without making ad hoc guesses about unknown variables. In general, we advocate taking the simplest approach to spatial modeling possible in each situation, while also recognizing that some conservation questions will demand a consideration of detailed spatial structure.

A Summary of the Problems

The models used by conservation biologists have become increasingly sophisticated. From life tables and species–area curves, analyses have moved to the consideration of metapopulation dynamics, environmental variation, nested subsets, and complicated habitat mosaics. Unfortunately, the utility of these analyses is often questionable, for two reasons. First, ecological situations and problems do not generalize well, and efforts to make sweeping statements about the kinds

of processes that will be important in all situations are unlikely to succeed (Estes et al., *in press*). Thus, a species or system may simply not operate in the way envisioned by the theories applied to it. This is particularly a problem when the latest conceptual fads in ecology are co-oped by conservationists eager to use them in an applied setting. Second, even potentially important theories or generalizations may be of little or no practical use to specific conservation problems, simply because it is impossible to estimate the relevant parameters with the data that are usually available. This is a greater problem in conservation than it is in basic research; analyses of specific species or areas must often be defended in the face of intense scrutiny (Dwyer 1992; Harrison et al., *in press*). Therefore, the need to have exact quantitative data to use a model accurately can be extremely limiting.

Both of these problems are exacerbated by statements asserting the preeminent importance of particular ecological models and theories for the assessment of population viability, for the preservation of biodiversity, and for the general understanding of conservation issues. Indeed, some biologists have set forth central "principles" of conservation biology that are almost given the status of holy writ.

SOLUTIONS

To effectively apply theory to conservation problem-solving, we must recognize both the practical and political limitations we face (Mills et al. 1993, Schemske et al. 1994). In light of these limitations, we make a few modest proposals to improve the role of theory in conservation:

1) We need more work on methods for estimating population and community parameters from incomplete data sets. The lack of data is the root cause of theory's prevalence in conservation arguments; using theory to make the most of what data are available is an obvious but under-appreciated role for theory to play. The work by Dennis et al. (1991) on the use of crude census data to extrapolate population trends provides an excellent example of this approach. Similarly, Minta and Mangel (1989) and Pollock et al. (1990) provide new methods to make the most out of limited and imperfect mark–recapture data, and Mangel and Tier (1994) provide new modeling techniques to better estimate persistence times. Lastly, Caswell's clear exposition of the advantages, pitfalls, and applications of matrix population models (Caswell 1989) serves to make a set of powerful and robust mathematical techniques available to a wide range of ecologists, including conservation biologists (e.g., Crouse et al. 1987).

2) Following from our last suggestion, theoreticians should also clearly state how data can be productively, and cheaply, collected to assess the importance of their favorite phenomena. Too often, theoreticians ignore the fact that the effective use of their work must rely upon data. If data are complete, then modeling can use them to make reliable predictions for management. If data are mediocre, then modeling may be useful in making qualitative predictions. And if data are poor, modeling may not be useful at all. An explicit acknowledgment of this gradient in discussions of theory would help field workers understand and assess the utility of particular modeling results.

3) Field workers should pay attention to the recommendations of the theoreticians and try to collect data that will be useful when parameterizing models, and otherwise testing the importance of plausible theoretical concerns. For example, consistency in the time intervals over which census data are gathered greatly increases their value (by allowing the calculation of spatial and temporal variation in life history parameters, as well as the degree of spatiotemporal correlation). However, budgetary constraints, bureaucratic interference, or lack of awareness of this simple point often lead to the collection of data that are substantially less useful than necessary (Chambers 1991). Also, as Schemske et al. (1994) document, management plans often call for the collection of data that have little or no direct relevance for the management of endangered species.

4) Modelers of real species or communities should seek to formulate the simplest models necessary to capture the relevant biological details of their system. While this seems a vague platitude, the increasing allure and power of GIS systems and canned population models are leading to more and more "realistic" models that are often too complex and too poorly parameterized to be useful. Unless complex models can be well supported by data, the curse of error propagation will overwhelm any advantage they have in increased "realism" (Ludwig and Walters 1985, Ludwig 1989).

We believe that all of the above concerns are of extreme practical value. If conservation biologists can make specific, well-supported recommendations and avoid general, untested "scientific" assertions, public and legal confidence in our pronouncements will remain high. While this strategy will certainly result in complicated, context-specific solutions, in our experience judges, lawyers and government bureaucrats are able to understand the complex, realistic arguments that pertain to most conservation decisions (e.g., Dwyer 1992). We agree with Brussard et al. (1992) that it is incumbent on us to teach such complexity to managers and nonbiologists, rather than attempting to snow them with undefendable over-generalizations.

Finally, we conclude by emphasizing that we do not advocate that conservation biologists become Luddites or simpletons. The pursuit of complicated theories of

population dynamics, community complexity, or spatial structuring is obviously healthy and useful for both ecology and conservation. These theories motivate the specific tests needed to understand new mechanisms and processes, and they expand the list of worries, concerns, and potential solutions that biologists should start with when considering a new conservation problem. Problems are created, however, when theoretical fashions create pet theories and pronouncements such as "metapopulation dynamics should always be considered." Advocating that these pet theories always be considered, or that they be codified into law (Rohlf 1991), ignores that many of our pets have short lives, and that others are like Pekinese—they are cute, but have no useful role in the real world.

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