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# Integrating the Metapopulation and Habitat Paradigms for Understanding Broad-Scale Declines of Species

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**Abstract:** *Caughley (1994) argued that researchers working on threatened populations tended to follow the “small population paradigm” or the “declining population paradigm,” and that greater integration of these paradigms was needed. Here I suggest that two related paradigms exist at the broader spatial scale, namely the metapopulation paradigm and habitat paradigm, and that these two paradigms also need to be integrated if we are to provide sound management advice. This integration is not trivial, and I outline five problems that need to be addressed: (1) habitat variables may not measure habitat quality, so site-specific data on vital rates are needed to resolve the effects of habitat quality and metapopulation dynamics; (2) measurements of vital rates may be confounded by movements; (3) vital rates may be density dependent; (4) vital rates may be affected by genotype; and (5) vital rates cannot be measured in unoccupied patches. I reviewed papers published in Conservation Biology from 1994 to 2003 and found 41 studies that analyzed data from 10 or more sites to understand the factors limiting species’ distributions. Five of the analyses presented were purely within the metapopulation paradigm, 14 were purely within the habitat paradigm, 17 involved elements of both paradigms, and 7 were theoretically ambiguous (2 papers presented 2 distinct analyses and were counted twice). This suggests that many researchers appreciate the need to integrate the paradigms. Only one study, however, used data on vital rates to resolve the effects of habitat quality and metapopulation dynamics (problem 1), and this study did not address problems 2–5. I conclude that more intensive research incorporating site-specific data on vital rates and movement is needed to complement the numerous analyses of distributional data being produced.*

**Key Words:** habitat quality, landscape ecology, population dynamics, spatial ecology, species recovery

Integración de los Paradigmas de Metapoblación y Hábitat para Entender la Declinación de Especies a Gran Escala

**Resumen:** *Caughley (1994) argumentaba que los investigadores de poblaciones amenazadas tendían a seguir el “paradigma de la población pequeña” o el “paradigma de la población declinante,” y que se necesitaba mayor integración de estos paradigmas. Aquí sugiero que, a escala espacial amplia, existen dos paradigmas relacionados, particularmente el paradigma de la metapoblación y el paradigma del hábitat, y que estos dos paradigmas también deben ser integrados si vamos a proporcionar consejos de manejo acertados. Esta integración no es trivial, y delíneo cinco problemas que deben ser atendidos: (1) puede que las variables de hábitat no midan la calidad del hábitat, por lo que se requieren datos sobre tasas vitales específicos de cada sitio para resolver los efectos de la calidad del hábitat y la dinámica de la metapoblación; (2) las medidas de las tasas vitales pueden estar enmascaradas por movimientos; (3) las tasas vitales pueden ser denso dependientes; (4) el genotipo puede afectar a las tasas vitales; y (5) las tasas vitales no pueden ser medidas en parches desocupados.*

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*Revisé artículos publicados en Conservation Biology entre 1994 y 2003 y encontré 41 estudios que analizaban datos de 10 o más sitios para entender los factores que limitan la distribución de especies. Cinco de los análisis presentados estaban dentro del paradigma de la metapoblación, 14 estaban en el paradigma del hábitat, 17 involucraban elementos de ambos paradigmas y 7 eran ambiguos teóricamente (dos artículos presentaron dos análisis distintos y fueron contados dos veces). Esto sugiere que muchos investigadores reconocen la necesidad de integrar los paradigmas. Sin embargo, solo un estudio utilizó datos de tasas vitales para resolver los efectos de la calidad del hábitat y la dinámica de la metapoblación (problema 1), y este estudio no abordó los problemas 2-5. Concluyo que se requiere más investigación intensiva que incorpore datos de tasas vitales y movimientos en sitios específicos para complementar los numerosos análisis de datos de distribución que se están produciendo.*

**Palabras Clave:** calidad de hábitat, dinámica poblacional, ecología de paisaje, ecología espacial, recuperación de especies

## Introduction

Caughley (1994) argues that two paradigms exist for understanding extinctions of populations, the “small population paradigm” and the “declining population paradigm.” He notes that the small population paradigm emphasizes factors threatening populations when they become small (i.e., demographic stochasticity, inbreeding depression, and Allee effects), whereas the declining population paradigm emphasizes the factors causing populations to decline in the first place (i.e., loss of habitat, overhunting, and introduction of exotic species). Caughley also argues that these paradigms are largely used in isolation of one another and that conservation biologists need to integrate them to achieve effective management of populations.

Caughley's paper has been widely read, cited, and debated (e.g., Hedrick et al. 1996; Young & Harcourt 1997; Asquith 2001) over the last decade, and I suggest that the two paradigms are now fairly well integrated by most conservation biologists. For example, population viability analysis (PVA) was cited by Caughley as a tool of the small population paradigm, but recent PVA literature strongly emphasizes comparison of strategies for managing the external factors causing population decline (Beissinger 2002). Although the small population paradigm and declining population paradigm have been integrated for single populations, I suggest that two related paradigms have emerged at a broader spatial scale, namely the metapopulation paradigm and habitat paradigm.

I outline these two paradigms and discuss why they need to be integrated if we are to provide sound management advice for halting broad-scale declines of species. This integration is not trivial, and I outline five problems that must be addressed for the effects of habitat quality and metapopulation dynamics to be resolved. I review papers published in *Conservation Biology* over the last decade to assess the extent to which these problems are being tackled in the literature.

## The Metapopulation Paradigm and Habitat Paradigm

In the last decade conservation biology has developed a strong emphasis on broad-scale conservation (e.g., Edwards et al. 1994). This emphasis has been facilitated by theoretical developments in macroecology (Brown 1995) and spatial dynamics (Tilman & Kareiva 1997; Bascompte & Solé 1998) but has also been necessitated by the realization that we need methods to tackle broad-scale problems. Two approaches have emerged for understanding broad-scale declines of individual species. Both approaches are quick to implement on a broad spatial scale, produce models explaining declines, and make clear predictions. The approaches are based on different theoretical paradigms, however, and both may lead to poor management if the underlying paradigm is invalid.

The first approach invokes the metapopulation paradigm, the essence of which is that populations are subject to chance extinction and that the proportion of patches occupied depends on extinction and colonization rates (Levins 1969). Levins' (1969) original concept involved an abstract set of patches that had identical extinction and colonization probabilities, but a range of models applicable to real landscapes have subsequently been developed (Gilpin & Hanski 1991; Hanski and Gilpin 1997; Hanski 1999). The basic assumptions of these models are that isolated patches have lower recolonization rates and that small populations are inherently vulnerable to extinction. The inherent vulnerability of small populations may be due to demographic stochasticity, inbreeding depression, and/or Allee effects but could also be due to emigration into the outside landscape (Basse & McLennan 2003). The incidence function model (ter Braak et al. 1998) is a particularly notable modeling approach because it allows a dynamic metapopulation model to be parameterized from a single snapshot of patch occupancy data. The classic example is Hanski et al.'s (1996) research on the butterfly *Milaetea cinxia*, for which the authors

parameterized the model from occupancy data for one portion of the landscape and showed that they could closely predict the level of occupancy in other areas. Such models can be used to predict how the level of patch occupancy will change under different management options (Drechsler et al. 2003).

The second approach invokes the habitat paradigm. Under the habitat paradigm, distributions are explained solely based on habitat characteristics (i.e., the species is assumed to be present where the habitat is suitable and absent where it is not). Habitat characteristics can include any feature of the environment relevant to a species, including human persecution and presence of introduced predators, competitors, or pathogens. This approach typically involves measuring several habitat variables followed by applying statistical techniques such as logistic regression, discriminant analysis, or artificial neural networks to distributional data to assess which variables are important (Manel et al. 1999; Guisan & Zimmermann 2000; Olden & Jackson 2002). Habitat variables may also be correlated with data on extinction and colonization. The approach is not new but has been revolutionized by the development of GIS techniques, which allow habitat variables to be measured remotely over large spatial scales (Donovan et al. 1987). It has also been made more powerful by recent statistical methods that allow detection probability to be taken into account (MacKenzie et al. 2003). The implicit assumption of this approach is that distributions are not affected by stochastic dynamics or connectivity. Thomas (1994) explicitly raised the habitat paradigm as an alternative to the metapopulation paradigm, arguing that extinctions and recolonizations are primarily due to changes in habitat suitability.

The metapopulation paradigm (MP) is an extension of Caughley's small population paradigm (SPP), whereas the habitat paradigm (HP) is an extension of the declining population paradigm (DPP) (Tables 1 & 2). The MP shares the SPP's idea that small populations are inherently vulnerable and extends the paradigm by incorporating the effect of isolation on colonization. The HP shares the DPP's idea that extinctions occur because of extrinsic factors (i.e., habitat) and extends the paradigm by explaining broad distributions. The SPP and MP are both relatively new ideas, the former becoming topical in the 1980s and the latter in the 1990s. The SPP and MP have a strong academic focus, coming from population ecologists and geneticists, whereas the DPP and HP have been primarily used by wildlife managers. The SPP and MP are theoretically innovative and elegant, whereas the DPP relies more on local knowledge and intuition of wildlife managers and the HP tends to use a shotgun approach. The elegance of the MP is facilitated by treating habitat quality in a simple way, making a simple distinction between suitable and unsuitable habitat. The HP has a strong focus on sophisticated habitat measurement and analysis at the expense of theoretical tractability.

**Table 1.** Characteristics of small and declining population paradigms for understanding extinction of populations, as outlined by Caughley (1994).

<i>Small population paradigm</i>	<i>Declining population paradigm</i>
extinction due to low numbers	extinction due to external factors (habitat)
developed in 1980s	traditional
from genetics and population ecology	from wildlife management
strong theory	weak theory "rooted in empiricism"
weak link to actuality	strong basis in problem solving

Analyses based on the metapopulation or habitat paradigms will both lead to management recommendations, so both approaches have clear practical value. The management recommendations are limited, however, by the underlying assumptions of the paradigms. The metapopulation paradigm assumes suitable patches may be unoccupied and isolation limits colonization. Analyses based on this paradigm may therefore recommend that corridors or stepping stones be established to facilitate movement (Beier & Noss 1998) or that reintroductions to unoccupied patches be considered (Armstrong & McLean 1995; Lubow 1996; Marsh & Trentham 2001). The habitat paradigm assumes distributions are determined solely by habitat quality, so analyses based on this paradigm will lead to recommendations to improve habitat quality (e.g., through predator control or revegetation). The IUCN (World Conservation Union) Guidelines for Reintroductions (IUCN 1998:6) are squarely within the habitat paradigm: they state that successful reintroduction requires "identification and elimination, or reduction to a sufficient level, or previous causes of decline," but this is not the case if reintroduction can be used on its own to ameliorate the effects of isolation.

Because the management recommendations depend on the paradigm followed, either approach may lead to the wrong answer if the paradigm is invalid. This could mean not only failure to identify a useful management

**Table 2.** Characteristics of metapopulation and habitat paradigms for understanding broad-scale declines of species.

<i>Metapopulation paradigm</i>	<i>Habitat paradigm</i>
extinction/colonization predicted by patch size & isolation	extinction/colonization predicted by habitat quality
developed in 1990s	traditional
population ecology, genetics	wildlife management, land management, geography
strong theory emphasizing dynamics	weak theory ignoring dynamics
habitat suitable or unsuitable	sophisticated habitat measurement and analysis

strategy but also adoption of deleterious management. The reason is that metapopulation and habitat factors are confounded. Habitat quality is frequently lower in small patches because of low diversity (Kindvall 1996), edge effects (Murcia 1995), and various physical factors (Saunders et al. 1991). Isolation may also be correlated with habitat quality because isolated remnants are usually left for a reason (e.g., poor soil) rather than at random. An analysis purely within the metapopulation paradigm might recommend reintroduction be used to recolonize small isolated patches, meaning organisms were released in poor habitat. Conversely, an analysis within the habitat paradigm could recommend management of an irrelevant habitat characteristic when the distribution was due to stochastic extinction and colonization.

### Problems to be Addressed for Integrating the Paradigms

The obvious solution to the confounding of habitat quality and metapopulation dynamics is to integrate the paradigms. If habitat quality can be measured accurately, the two paradigms can be integrated by producing a model in which occupancy is predicted by a combination of habitat quality, patch size, and isolation. Measuring habitat quality is rarely straightforward, however, and can lead to five problems that need to be addressed in integrating the paradigms: (1) habitat variables may not measure habitat quality, so site-specific data on vital rates are needed to resolve the effects of habitat quality and metapopulation dynamics; (2) measurements of vital rates may be confounded by movements; (3) vital rates may be density dependent; (4) vital rates may be affected by genotype; and (5) vital rates cannot be measured in unoccupied patches.

#### Habitat Variables May Not Measure Habitat Quality

Because measuring habitat quality is not straightforward, researchers often take the shotgun approach in measuring many habitat variables in the hope of finding some that are important. The shotgun approach may result in an overfitted habitat model, meaning irrelevant variables are identified as being important. Such overfitting is inevitable in analyses of multiple variables, especially when techniques such as stepwise logistic regression are used to allow thousands if not millions of potential models to be considered (Burnham & Anderson 2002). The shotgun approach may, however, also result in an underfitted model if the important habitat variables are not measured. Such underfitting is likely if the variables are chosen based on ease of measurement (e.g., via GIS data) rather than their likely ecological significance. When combined with data on patch size and isolation, an overfitted habitat model will result in habitat quality being overempha-

sized, whereas an underfitted habitat model will result in metapopulation dynamics being overemphasized. This problem cannot be overcome through any analysis of occupancy or other distributional data. It can only be overcome by directly measuring habitat quality for the species concerned, meaning that vital rates (reproduction and survival) must be estimated at individual sites.

#### Measurements of Vital Rates May Be Confounded by Movement

Although vital rates provide the only direct measure of habitat quality, data must be interpreted with care because of confounding factors (problems 3–4) and measurement bias. The most obvious measurement bias is that emigrating organisms may be assumed to have died (reducing the measured survival rate) or may not be detected at all (reducing the measured recruitment rate). Populations occupying small areas of suitable habitat may suffer from high rates of emigration to the surrounding landscape (Basse & McLennan 2003). If this is not accounted for, such populations will be assumed to have poor survival or recruitment. Consequently, an effect of metapopulation dynamics will be mistaken for poor habitat quality. Emigration can be accounted for by combining data on dead recoveries with data on live sightings or recaptures, by extending searches or trapping grids to detect dispersing individuals, or by using techniques such as radiotelemetry to obtain known-fate data (Nichols et al. 1993). A bonus of obtaining radiotelemetry data is that realistic dispersal behavior can be incorporated into metapopulation models instead of assuming movement probability is a simple function of distance.

#### Vital Rates May Be Density Dependent

The first factor that may confound the relationship between habitat quality and vital rates is density dependence. As populations increase in density, at some stage decreased reproduction or survival or increased emigration must result (Turchin 1999). The effect of density can be accounted for when measuring habitat quality, but this requires sufficient research on the species to understand how its populations are regulated. Some researchers use density alone as a proxy measure of habitat quality (e.g., Foppen et al. 2000). Density may be poorly correlated with habitat quality (van Horne 1983), however, and in some cases the highest densities occur in poor-quality sink habitats (Brawn & Robinson 1996).

#### Vital Rates May Be Affected by Genotype

The other confounding factor is that vital rates may be affected by the intrinsic quality of the individuals in the population as well as the habitat. Random variation among individuals can be accounted for by including individual as a random factor in analyses. If populations have been

highly isolated, however, overall differences in genetic quality may result (e.g., small populations could have lower reproductive rates because of inbreeding depression) (Frankham & Ralls 1998). Studying this problem requires introducing inbreeding as another factor to be measured. Indices such as fluctuating asymmetry should not be used because they may be correlated with habitat quality as well as inbreeding (Lens & Van Dongen 2002).

### **Vital Rates Cannot Be Measured in Unoccupied Patches**

This is the most difficult problem. Although we need data on vital rates to determine unambiguously why a species is absent from some sites, such data are unavailable because the species is absent. The ideal solution is reintroduction to unoccupied patches. Such an experiment, however, requires sufficient patches and sufficient monitoring to enable a robust comparison of vital rates between previously occupied and newly occupied patches. The fact that animals are able to survive and breed following reintroduction (cf. Cooper & Walters 2002) does not imply long-term viability and does not in itself provide information on the roles of habitat quality and metapopulation dynamics in the original extinctions. Given that there will be few opportunities for robust reintroduction experiments, we need alternative approaches to this problem.

First, we can stop trying to explain why species are absent from some sites and instead focus solely on conservation of extant populations. Data on vital rates can be used to measure quality of patches with extant populations, and demographic modeling can be used to estimate extinction probabilities as a function of vital rates and patch sizes. Colonization probabilities can be estimated directly from movement data rather than from patterns of occupancy. These can be combined into spatially realistic metapopulation models that can be used to predict the pattern of future loss under different management scenarios.

Second, key habitat variables can be measured in occupied patches when vital rates are measured. If habitat quality is predictable based on the variables measured, then this model can be extrapolated to unoccupied patches.

Third, proxy data on vital rates can be collected in unoccupied patches. For example, population growth rates of many bird species are closely correlated with nest predation (Newton 1998), meaning artificial nest experiments (Faaborg 2004; Villard & Pärt 2004) could be used to estimate habitat quality of unoccupied patches if it can be demonstrated that artificial nests give an accurate index of real predation rates.

### **Papers in *Conservation Biology*, 1994–2003**

I read papers published in *Conservation Biology* in the decade since Caughley's article to assess the degree to

which the metapopulation and habitat paradigms have been integrated and the extent to which the problems I outline above have been addressed. My objective was not to provide a comprehensive meta-analysis of trends; hence, I focused on one journal to allow characteristics of individual papers to be noted and discussed. In addition, my criteria for selecting papers could not be achieved through a set of keywords because the wording used in the titles and abstracts varied greatly among papers. I selected papers that reported distributional data for one or more species in at least 10 separate sites and reported analyses to explain those distributions. I did not include papers reporting community-level properties such as species richness or diversity unless they also included data for individual species.

Of the 41 papers meeting the above criteria, 5 presented analyses purely within the metapopulation paradigm, 14 presented analyses purely within the habitat paradigm, 17 presented analyses involving elements of both paradigms, and 7 were theoretically ambiguous (Table 3). Two of the papers (Quintana-Ascencio & Menges 1996; Akcakaya & Atwood 1997) are counted twice because they report two types of analyses. In both cases, a dynamic metapopulation model was accompanied by a static model analyzing occupancy with respect to habitat variables. The 7 ambiguous papers considered "area sensitivity" alone (i.e., examined distributional data with respect to patch size only). This approach produces ambiguous results in terms of management because it is unclear whether the correlations are due to stochastic extinctions, habitat quality, or both.

Although most (31) of the papers measured habitat variables, the approach to habitat varied tremendously. Some analyses focused on a single habitat variable known to be important for the species (successional stage: Dupuis et al. 1995; Skelly & Meir 1997; Crooks et al. 2001; grazing: Norton et al. 1995; fire: Quintana-Ascencio & Menges 1996; stream flow: Lafferty et al. 1999), and one analysis incorporated data on 4 key habitat variables into a metapopulation model (Lawes et al. 2000). Such approaches give some confidence that researchers have arrived at a reliable understanding of the roles of both habitat quality and metapopulation dynamics. Most analyses, however, included at least 7 habitat variables, and four analyses considered the effect of more than 20 variables through the use of stepwise logistic regression (Fielding & Haworth 1995; Bakker et al. 2002; Fleishman et al. 2002) or a separate analysis of variance for each variable (Balcom & Yahner 1996). Such approaches must be viewed as exploratory (Fielding & Haworth 1995), with further research needed to obtain a reliable understanding of habitat quality and to integrate the habitat and metapopulation paradigms.

Only eight papers included data related to vital rates, with three reporting nest success, five reporting both survival and/or reproduction, and one reporting population

**Table 3.** Papers from *Conservation Biology* 1994–2003 reporting distributional data for at least 10 sites, showing whether the data used to analyze those distributions follows the metapopulation paradigm, the habitat paradigm, or an integration of the two.

Paper	Taxon <sup>a</sup>	Distinct patches	Distribution data <sup>b</sup>	Patch size	Patch isolation	Dynamic model	Habitat variables	Vital rates <sup>c</sup>	Paradigm <sup>d</sup>
Short & Turner 1994	mammals	no	D				X	F	H
Vickery et al. 1994	birds	yes	O	X			X		H/M
Bancroft et al. 1995	birds	yes	O	X					
Breining et al. 1995	bird	no	D				X	S, F, NS	H
Donovan et al. 1995	birds	yes	D	X				NS	
Dunning et al. 1995	bird	yes	C		X				M
Dupuis et al. 1995	amphibians	yes	D	X			X		H/M
Fielding & Haworth 1995	birds	no	O				X		H
Knick & Rotenberry 1995	birds	no	O				X		H
Mills 1995	mammals	yes	D	X					
Norton et al. 1995	plant	yes	D	X			X		H/M
Schieck et al. 1995	birds	yes	D/O	X					
Balcom & Yahner 1996	mammal	yes	O				X		H
Hanski et al. 1996	butterfly	yes	O	X	X	X			M
Quintana-Ascencio & Menges 1996 <sup>e</sup>	plants	yes	O	X	X	X			M
			O	X	X		X		H/M
Akçakaya & Atwood 1997 <sup>e</sup>	bird	yes	O	X	X	X		S, F	M
			O				X		H
Skelly & Meir 1997	amphibians	yes	E/C		X		X		H/M
Smith et al. 1997	mammals	no	D				X		H
Saari et al. 1998	bird	yes	O/E/C	X			X		H/M
Beard et al. 1999	birds	no	O				X		H
Carroll et al. 1999	mammal	no	O				X		H
Corsi et al. 1999	mammal	no	O				X		H/M
Lafferty et al. 1999	fish	yes	E/C	X	X		X		H/M
Rosenberg et al. 1999	birds	yes	O	X	X		X		H/M
Winter & Faaborg 1999	birds	yes	D	X			X	NS	H/M
Foppen et al. 2000	bird	yes	D/O	X	X	X	X		H/M
Lawes et al. 2000	mammals	yes	O	X	X	X	X		H/M
Lunney et al. 2000	mammal	no	O				X		H
van der Haegen 2000	birds	no	O				X		H
Crooks et al. 2001	birds	yes	E	X	X		X		H/M
Fleishman et al. 2001	butterflies	yes	O				X		H
Hokit et al. 2001	lizard	yes	O	X	X	X		S, F	M
Joly et al. 2001	amphibians	yes	O	X	X		X		H/M
Singer et al. 2001	mammal	yes	E	X				$\lambda$	
Bakker et al. 2002	birds	yes	O	X	X		X		H/M
Fleishman et al. 2002	butterfly	yes	O/E/C	X	X		X		H/M
Guerry & Hunter 2002	amphibians	yes	O	X					
Lowe & Bolger 2002	amphibians	yes	D		X		X		H/M
Hemstrom et al. 2002;	bird	no	O				X		H
Wisdom et al. 2002a, 2002b									
Carroll et al. 2003	mammal	no	D/O				X	S, F	H
Kurosawa & Askins 2003	birds	yes	D	X					

<sup>a</sup>Singular (e.g., bird, fish) indicates one species, plural (e.g., birds) indicates multiple species.

<sup>b</sup>Abbreviations: O, occupancy; D, density; E, extinction; C, colonization.

<sup>c</sup>Abbreviations: NS, nest success; S, survival; F, fecundity or fertility;  $\lambda$ , population growth rate.

<sup>d</sup>Abbreviations: H, habitat paradigm; M, metapopulation paradigm; H/M, integration of two paradigms (cells left blank show paradigm is ambiguous).

<sup>e</sup>Two analyses with different approaches are reported; hence, a different row is shown for each analysis.

growth rates (Table 3). Four studies reported how these rates changed with patch size (Donovan et al. 1995; Winter & Faaborg 1999; Singer et al. 2001; Hokit et al. 2001), and three reported how they changed with habitat type (Short & Turner 1994; Breining et al. 1995; Carroll et al. 2003). Hokit et al. (2001) incorporated vital rates for large

and small patches into a spatially explicit metapopulation model, and this was the only attempt to use vital-rate data to resolve the potential confound between habitat quality and metapopulation dynamics (problem 1). The estimates used, however, did not seem to account for emigration (problem 2), meaning the apparently lower survival

and recruitment in small patches may have been due to metapopulation dynamics rather than to small patches being of lower quality.

## Conclusions

A reasonable proportion of the studies I examined considered both habitat and metapopulation factors when explaining distributional data. Of the 41 studies, 3 reported changes in density over areas where the species had relatively continuous distributions, so we would not expect metapopulation dynamics to be relevant. Of the remaining 38 studies, almost half (17) made some attempt to integrate the habitat and metapopulation paradigms, and very few operated purely within the metapopulation paradigm.

The majority of studies, however, took a shotgun approach to analyzing habitat, giving little confidence that habitat quality could be measured accurately and integrated with metapopulation dynamics. Few studies provided data on vital rates, and only one attempted to use these data to resolve the potential confound between habitat quality and metapopulation dynamics. Therefore, although many researchers clearly see the need to integrate the habitat and metapopulation paradigms when explaining broad-scale declines of species, the research published in *Conservation Biology* over the last decade does not address the problems outlined above. Addressing these problems requires studies that incorporate site-specific data on vital rates and movements into analyses of distributional data.

The need for such intensive data collection may seem to contradict our need to address conservation problems rapidly and on a broad spatial scale. I see three solutions, however, to this dilemma. First, where previous research has been conducted on a species, one or two relatively simple parameters might be found to accurately predict population growth rate, and these can be used as reliable measures of habitat quality to be integrated with metapopulation dynamics. For example, the key factor accounting for declines of some New Zealand forest birds is low nest success due to predation by introduced mammals, and nest success may be closely correlated with simple indices of predator abundance (Innes et al. 1999). Second, where little is known about a species, necessitating a shotgun approach to habitat quality, analyses attempting to integrate habitat quality and metapopulation dynamics should be treated as exploratory. The conclusions reached should therefore be treated as hypotheses, and the management based on those conclusions designed to test those hypotheses. Finally, where analyses are being conducted for multiple species, a subset of species should be selected for intensive data collection to address the problems I outlined. We need to achieve the right balance so we can continue to produce the analyses needed

to tackle broad-scale conservation problems but ensure that those analyses are generally reaching the right conclusions.

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