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An empirical evaluation of the area and isolation paradigm of metapopulation dynamics

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ARTICLE INFO

Article history:

Received 27 September 2006

Received in revised form

19 December 2006

Accepted 21 December 2006

Available online 22 February 2007

Keywords:

Butterflies

Amphibians

Birds

Speyeria nokomis

Maculinea nausithous

Bufo calamita

Hyla arborea

Selasphorus platycercus

Picoides villosus

Troglodytes aedon

Dendroica petechia

Melospiza melodia

Passerina amoena

Switzerland

Great Basin

Extinction

Colonization

Connectivity

Patch area

ABSTRACT

Much of metapopulation theory assumes that the persistence of individual populations in a metapopulation, and persistence of the metapopulation as a whole, is best modeled by the area of habitat patches and their isolation. Estimates of isolation typically include a measure of geographic distance and a measure of either population size or patch area. This “area and isolation paradigm” assumes a functional relationship between the area of a patch and its extinction probability, and between isolation of a patch and its colonization probability. Although these assumptions are fundamental to use of incidence function models of metapopulation dynamics, the assumptions have been validated in only a small number of studies. We tested the ability of area and isolation to predict extinction and colonization patterns using multiple-year occupancy data for 10 species from three taxonomic groups (butterflies, amphibians, and birds). We examined 13 potential models of metapopulation dynamics. All models included four basic parameters: occupancy during the first year of the survey, probability of extinction, probability of colonization, and single-visit detection probability. In eight models, each parameter was either constant or time-dependent. Five models included a patch-level covariate of extinction probability (patch area or population size), colonization probability (connectivity, the inverse of isolation), or both. Extinction patterns generally were predicted more effectively as a function of local population size than as a function of patch area, a constant probability of extinction, or a time-dependent probability of extinction. In most cases, inclusion of connectivity as a patch-level covariate did not improve predictions of colonization patterns. We estimated single-visit detection probabilities for all species in our analyses, thus providing evidence-based guidelines for the refinement of future monitoring protocols.

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doi:10.1016/j.biocon.2006.12.020

1. Introduction

Many species naturally occur as ephemeral local populations in patches of habitat distributed across a landscape matrix that is otherwise unsuitable for the species (Levins, 1969). When such networks are maintained through dispersal and colonization, they are referred to as metapopulations (Hanski, 1998; Hanski and Gaggiotti, 2004). Evidence of metapopulation structure has been found in multiple taxonomic groups, among which butterflies (Dennis and Eales, 1999; Fleishman et al., 2002; Hanski and Gaggiotti, 2004), amphibians (Sjögren-Gulve and Ray, 1996; Pope et al., 2000; Vos et al., 2000; Marsh and Trenham, 2001), and birds (Erwin et al., 1998; Akçakaya et al., 2004) provide well-studied examples.

The conservation of imperiled species that exhibit metapopulation structure is becoming increasingly challenging on human-dominated landscapes. In these situations, patches of habitat are being lost, fragmented, and separated (isolated) as both the patches and the matrix are transformed by various land uses (McCullough, 1996; Akçakaya and Sjögren-Gulve, 2000; Beissinger and McCullough, 2002). A number of tools have been used to assess probabilities of metapopulation persistence, or to explore alternative patch-based strategies to conserve metapopulations. Patch occupancy models, for example, predict the number or proportion of patches in a metapopulation that are occupied by the focal species at a given time step. Many patch occupancy models also estimate probabilities of extinction and colonization for each patch; these probabilities can be incorporated into simulations to predict metapopulation persistence over time. Patch occupancy models are popular among researchers and practitioners because their data requirements are relatively modest: the location and size of habitat patches and whether the species is present or absent in each patch for at least one complete inventory or time step (Hanski, 1994; Sjögren-Gulve, 1994; Sjögren-Gulve and Ray, 1996; Vos et al., 2000; Pellet et al., 2006).

Patch occupancy models are derived from the area and isolation paradigm. This paradigm assumes that the presence and survival of individual populations in a metapopulation, and the persistence of the metapopulation as a whole, is best modeled by the area of habitat patches and the isolation of patches (Hanski, 1994, 1998, 1999; Moilanen, 1999; Hanski and Ovaskainen, 2000; Hanski and Gaggiotti, 2004; Ovaskainen and Hanski, 2004). Isolation ideally refers not simply to distance from a given patch, or the population it supports, to the nearest neighboring patch or local population, but to distance from all extant populations that might serve as sources of colonists (Hanski, 1999). Measures of isolation also may incorporate information on population size or the ease with which individuals can disperse through the matrix. Patch area is assumed to be correlated with population size, and both in turn to be correlated with extinction risk. The area and isolation paradigm thus assumes that the probability of population extinction decreases as the area of a habitat patch increases, and that the probability of patch colonization increases as isolation decreases. If these two assumptions are true, the dynamic metapopulation processes of extinction and colonization can be related directly by conservation planners to the sizes and locations of patches that collectively support metapopulations of concern.

The locations, sizes, and occupancy states of habitat patches in a metapopulation can be determined on the basis of field surveys. Estimating the relative importance of patch area and isolation on probabilities of extinction and colonization is challenging, however, because data on the processes that drive extinction and colonization dynamics often are difficult to obtain. Patch occupancy, a binary state variable describing the patch as occupied or vacant, is therefore frequently used to infer local extinction and colonization probabilities on the basis of logistic regression (Etienne et al., 2004), incidence function models (Hanski, 1992, 1994; Ter Braak et al., 1998; Vos et al., 2000), or Bayesian approaches (O'Hara et al., 2002; Ter Braak and Etienne, 2003). These methods have been applied successfully to a range of species, but each has at least one of two disadvantages. First, they assume that a given species is always detected in a patch where it is present. Second, the methods assume that metapopulations are at Markovian pseudo-equilibrium (Hanski, 1998; Etienne et al., 2004), meaning that the occupancy status of each patch at time $t + 1$ is dictated solely by patch status at time t (Moilanen, 1999; Barbraud et al., 2003).

Detection probability is recognized as a central issue in biological inventories, reflecting the fact that resident populations are not always detected during field surveys (Bart and Schoultz, 1984; MacKenzie et al., 2002; Moilanen, 2002; Gu and Swihart, 2004; Pellet and Schmidt, 2005). Imperfect detection introduces bias in occupancy data because apparent absence of a population from a surveyed patch can mean either that the patch indeed is vacant, or that the population is present but not detected. If the patch state is recorded as occupied in time steps $t - 1$ and $t + 1$, but is incorrectly recorded as vacant in time step t , that false-negative would lead to the erroneous conclusion that the population had been extirpated and then subsequently the patch was recolonized, when in reality the patch had been occupied across the time sequence. It has been demonstrated that false absences result in overestimates of both extinction probabilities and dispersal abilities of species that survive in metapopulations (Moilanen, 2002). Partly in response to that concern, a method that allows detection probabilities to be explicitly incorporated into metapopulation models was developed recently (MacKenzie et al., 2003).

The second assumption of most patch occupancy models, that the metapopulation is at pseudo-equilibrium, generally is difficult to test (but see Moilanen, 2002); therefore, we believe it is wise to assume nothing about the equilibrium state of the metapopulation. This assumption-free approach has been successfully used by Erwin et al. (1998) and Moilanen (1999), although neither study accounted for imperfect detectability. In this paper, we explore new methods based on robust statistical designs that can be used to relax both the steady-state and perfect detectability assumptions (MacKenzie et al., 2003, 2006). These modeling approaches are similar to Pollock's robust design for mark-recapture experiments, where each patch is visited k times during each of t years (Pollock, 1982). Patches are assumed to be closed (either occupied or vacant) within years, but open between years, allowing for colonization and extinction events to occur. At each visit, patch occupancy is assessed, resulting in a binary detection history of zeros (absences) and ones (presences) across multi-

ple years. The analytic framework then explicitly includes detection probability as a variable before estimating probabilities of extinction and colonization through likelihood maximization.

Although widely used in conservation, metapopulation models are based on multiple simplifying assumptions that rarely have been validated empirically. Here we evaluate the circumstances under which the area and isolation paradigm can serve as a tool for better understanding metapopulation dynamics and informing conservation planning. We apply 13 different models to metapopulation occupancy data for 10 species of butterflies, amphibians, and birds. Four parameters – occupancy during the first year of the survey, probability of colonization, probability of extinction, and single-visit detection probability – are included in all models. In different models, these parameters are either constant or time-dependent. Five of the models include one or two patch-level covariates: area, population size, and connectivity (the inverse of isolation). By applying the full set of models, we examine whether the cost of collecting data to estimate time-dependent and patch-specific parameters is worthwhile in terms of our ability to forecast changes in metapopulation occupancy, the proportion of patches in which the species is present over time. We also explore whether patch area is an effective surrogate measure of population size. Further, we estimate single-visit detection probabilities for each of the 10 species. This allows us to examine the potential effects of detectability on inferences about metapopulation dynamics and appropriate conservation planning for a given species.

2. Methods

Each of 10 species in our analyses had resource requirements that were sufficiently specialized to allow spatial delineation of patches of habitat. During the time period in which surveys were conducted, each species also had asynchronous extinction of local populations and recolonized multiple patches of habitat. We examined data for two species of butterflies, *Speyeria nokomis* and *Maculinea nausithous*; two species of amphibians, *Hyla arborea* (European tree frog) and *Bufo calamita* (natterjack toad); and six species of birds, *Selasphorus platycercus* (Broad-tailed Hummingbird), *Picoides villosus* (Hairy Woodpecker), *Troglodytes aedon* (House Wren), *Dendroica petechia* (Yellow Warbler), *Melospiza melodia* (Song Sparrow), and *Passerina amoena* (Lazuli Bunting).

2.1. Occurrence data

S. nokomis occupies seeps, springs, and other riparian areas in the central Great Basin (Nevada, USA) where its larval host plant, *Viola nephrophylla*, grows with its adult nectar sources, *Cirsium* spp. and *Carduus* spp. (Fleishman et al., 2002). Our analyses included data collected from 1995 to 1998 in a network of 39 patches in the Toiyabe Range (Table 1). Each patch was visited an average of 5.3 times (SD = 1.1) per year, for a total of 827 visits. The myrmecophilous butterfly *M. nausithous* occurs along the southern shore of Lake Neuchâtel, Switzerland. The species is associated with wet grasslands in which both its host plant (*Sanguisorba officinalis*) and ant nests (*Myrmica rubra*) are present. Due to the localized nature of these

Table 1 – Attributes of metapopulations included in analyses

Taxonomic group	Species	Region	Years monitored	Number of patches	Naïve occupancy ± SD	Mean distance to closest patch (km) ± SD	Mean interpatch distance (km)
Butterflies	<i>Speyeria nokomis</i>	Great Basin, Nevada, USA	1995–1998	39	0.583 ± 0.252	0.8 ± 1.1	20.0 ± 14.1
	<i>Maculinea nausithous</i>	Grande Carrière, Switzerland	1997–2005	15	0.900 ± 0.113	1.8 ± 1.0	13.6 ± 8.8
Amphibians	<i>Bufo calamita</i>	La Côte, Switzerland	2002–2005	27	0.426 ± 0.071	1.7 ± 1.1	7.0 ± 3.8
	<i>Hyla arborea</i>				0.611 ± 0.048		
Birds	<i>Selasphorus platycercus</i>	Great Basin, Nevada, USA	2001–2004	12	0.542 ± 0.259	6.2 ± 3.7	36.0 ± 19.0
	<i>Picoides villosus</i>				0.292 ± 0.108		
	<i>Troglodytes aedon</i>				0.375 ± 0.108		
	<i>Dendroica petechia</i>				0.458 ± 0.144		
	<i>Melospiza melodia</i>				0.500 ± 0.118		
	<i>Passerina amoena</i>				0.375 ± 0.083		

The naïve occupancy is the mean proportion of patches in which the species was detected each year.

grasslands, individuals are aggregated in 15 separate meadows. The species is easy to detect with visual surveys; we visited each patch an average of 2.3 times per year ($SD = 0.8$) from 1997 to 2005, for a total of 311 site visits.

The endangered species *H. arborea* and *B. calamita* are associated with early successional wetlands in western Switzerland (Schmidt and Zumbach, 2005). The conspicuous calling behavior of breeding males makes them easy to detect and thus counts of breeding males are the preferred monitoring technique (Heyer et al., 1994; Carlson and Edenhamn, 2000; Pellet and Schmidt, 2005). Presence or absence of both species was monitored in 27 patches from 2002 to 2005 (Pellet, 2005). A total of 392 site visits was included in these analyses (Table 1). Ponds were visited an average of 3.6 times ($SD = 1.9$) each year.

Bird data used in these analyses were collected from 2001 through 2004 in three adjacent mountain ranges in the central Great Basin that have similar biogeographic and human land-use histories, the Shoshone Mountains, Toiyabe Range, and Toquima Range. Data from 12 canyons are included in the analyses presented here. We restricted our analysis to species that are largely or entirely restricted to riparian habitats (Dobkin and Wilcox, 1986), with intermediate patch occupancy (20–80%) across years and at least one apparent turnover event (population extirpation or colonization) each year. Data for 144 site visits were included in our analyses (Table 1). Data collection used established techniques that are believed to detect species presence reliably and allow assessment of distributional trends (Bibby et al., 2000). We provide an abbreviated description here; these methods have been described in detail previously (Dobkin and Wilcox, 1986; Mac Nally et al., 2004).

Birds were sampled during the breeding season (late May through June) using two or three 75-m variable-radius point counts per hundred meters of vertical elevation change. Most point centers were at least 350 m apart. Point counts are an effective method of sampling birds in riparian areas in the Great Basin (Dobkin and Rich, 1998). Within a canyon, points were located in each of the dominant vegetation types (e.g., aspen, willow, mixed pinyon-juniper woodland, wet meadow, sagebrush). During each visit, all birds actively using terrestrial habitat within the point were recorded by sight or sound. Point counts were conducted only in calm weather, and none were conducted >3.5 h after dawn. Each point was visited three times per year for 5 min per visit.

2.2. Patch-specific covariates

For butterflies, habitat patches were delineated on the basis of land cover and presence of larval host plants. Annual population sizes for each patch, defined as the number of adults in the patch in a given year, were estimated as the maximum number of adults detected in the patch on any day in that year.

Habitat patches for amphibians were defined as breeding ponds, and patch area was estimated as the surface area of the pond. Annual population sizes for each patch were estimated from the maximum number of calling males heard on any one night in that year (Carlson and Edenhamn, 2000; Schmidt and Pellet, 2005).

For birds, patch area was estimated as the length of the riparian corridor within each canyon; the width of the corridor rarely exceeded 100 m. Habitat for riparian-obligate birds in this system typically is confined to canyon bottoms, which are separated by steep uplands with limited resources. Annual population sizes for each patch were estimated as the maximum number of individuals detected on any given day in that year.

For all species, the average population size for each patch across the multiple-year sampling period was estimated as the mean annual population size for the patch.

In a metapopulation context, connectivity – the inverse of isolation – is a patch-specific parameter that typically refers to the number of immigrants arriving to a patch from all other patches in a network (Hanski, 1999). Measures of connectivity incorporate both attributes of the landscape in which the metapopulation is embedded and attributes of the focal species. We computed connectivity of each patch as $connectivity_i = \sum_{j \neq i} e^{-\alpha d_{ij}} N_j$, where N_j is population size of patch j , d_{ij} the distance between patches i and j , and $1/\alpha$ is the mean dispersal distance of the focal species (see Hanski, 1999, p. 217). Other measures of connectivity have replaced population size with either patch area or a binary occupancy variable (Hanski, 1994; Vos et al., 2000). We included population size explicitly because we believed this measure is more appropriate to predict the number of migrants between patches.

The mean dispersal distance $1/\alpha$ for each species was estimated using all available data. Mark-recapture data on *S. nokomis* detected dispersal distances up to 4 km (Fleishman et al., 2002). Mean dispersal distance, however, was approximately 600 m. For *M. nausithous*, mean dispersal distance is believed to be several hundred meters (Nowicki et al., 2005). We estimated the mean dispersal distance for both butterflies as 600 m.

Most recorded dispersal distances of *H. arborea* (Vos et al., 2000) are less than 1.5 km. We estimated mean dispersal distance for *H. arborea* as 1 km. *B. calamita* is known to have dispersal distances up to 2 km (Sinsch, 1997), but reliable estimates of mean dispersal distance are not available. Therefore, we estimated the mean dispersal distance for this species as 1 km.

Mean dispersal distance for birds was estimated to be 10 km, approximately the mean distance among neighboring patches. Few data on among-breeding season dispersal distances are available for most species of birds in North America (Walters, 2000), especially for relatively small-bodied birds such as those in our study.

2.3. Data analysis

We developed a set of 13 candidate models of metapopulation dynamics that included four parameters with varying degrees of complexity (Table 2). All models were applied to each of our 10 sets of occupancy data. This process allowed us to examine how the accuracy of predictions of metapopulation occupancy is affected by use of constant versus time-dependent parameters and by inclusion of patch-level covariates. Use of these models also facilitated exploration of whether patch area is an effective surrogate measure of population size. We

Table 2 – Candidate models of metapopulation dynamics

Model	Model function
1	$\psi(\text{year1})\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$
2	$\psi(\text{year1})\gamma(t)\varepsilon(\cdot)p(\cdot)$
3	$\psi(\text{year1})\gamma(\cdot)\varepsilon(t)p(\cdot)$
4	$\psi(\text{year1})\gamma(t)\varepsilon(t)p(\cdot)$
5	$\psi(\text{year1})\gamma(\cdot)\varepsilon(\cdot)p(t)$
6	$\psi(\text{year1})\gamma(t)\varepsilon(\cdot)p(t)$
7	$\psi(\text{year1})\gamma(\cdot)\varepsilon(t)p(t)$
8	$\psi(\text{year1})\gamma(t)\varepsilon(t)p(t)$
9	$\psi(\text{year1})\gamma(\text{connectivity})\varepsilon(\cdot)p(\cdot)$
10	$\psi(\text{year1})\gamma(\cdot)\varepsilon(\text{patch area})p(\cdot)$
11	$\psi(\text{year1})\gamma(\cdot)\varepsilon(\text{population size})p(\cdot)$
12	$\psi(\text{year1})\gamma(\text{connectivity})\varepsilon(\text{patch area})p(\cdot)$
13	$\psi(\text{year1})\gamma(\text{connectivity})\varepsilon(\text{population size})p(\cdot)$

$\psi(\text{year1})$ is the occupancy during the first year of the survey, $\gamma(\cdot)$ the probability of colonization, $\varepsilon(\cdot)$ the probability of extinction, and $p(\cdot)$ is the single-visit detection probability of the species. Potential factors affecting colonization and extinction probabilities are effective connectivity, patch area, and population size.

used a multiple-season occupancy modeling framework (as implemented in PRESENCE, available for download from www.proteus.co.nz) that accounts for detection probability (MacKenzie et al., 2003, 2006). All models had the form $\psi(\text{year1})\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$, where $\psi(\text{year1})$ is occupancy (the proportion of patches in which the species was present) during the first year of the survey, $\gamma(\cdot)$ is the probability of colonization, $\varepsilon(\cdot)$ is the probability of extinction, and $p(\cdot)$ is the single-visit detection probability of the species (Fig. 1). The covariates for each parameter are indicated within parentheses. Dots indicate constants, and t indicates a time-dependent (year-dependent) parameter. Patch area and population size were included as covariates of extinction probability, and connectivity was included as a covariate of colonization probability.

We first constructed a set of eight models in which each parameter – occupancy during the first year of the survey, probability of colonization, probability of extinction, and sin-

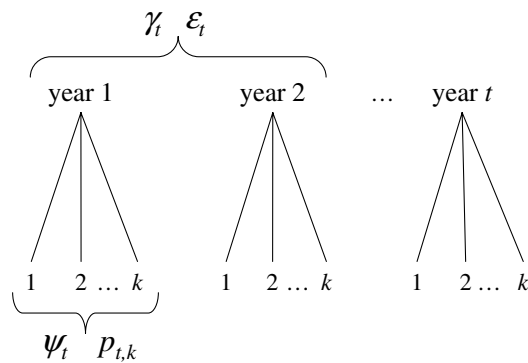


Fig. 1 – Illustration of the framework for occupancy modeling (adapted from Bailey et al. (2004)). During each year t , each patch is visited k times. Probabilities of colonization (γ) and extinction (ε) are estimated between years, whereas probabilities of patch occupancy (ψ) and detection (p) are estimated within each year.

gle-visit detection probability – was either constant or time-dependent in every possible combination (models 1–8, Table 2). In model 1, for example, probability of extinction was assumed to be constant over time [$\varepsilon(\cdot)$], whereas in model 3 the probability of extinction was assumed to change each year [$\varepsilon(t)$]. We did not construct models with survey-specific detection probabilities, because these models would have included far more parameters than reasonable given our data. Model selection on this first set of eight models indicated that detection probability consistently was modeled best as a constant. We thus set detection probability as constant in five subsequent models. These five models included either one or two patch-level covariates in every possible combination. Two parameters (patch area and population size) covaried with extinction, and one parameter (connectivity) covaried with colonization. Models 9, 10, and 11 included a covariate for either extinction or colonization, whereas models 12 and 13 contained a covariate for both extinction and colonization (Table 2).

As with capture–recapture methods, we derived model likelihood from species detection histories (MacKenzie et al., 2002). A detection history for a given patch documents whether a species was observed (1) or not observed (0) during each visit. A within-year detection history of “101,” for example, would indicate that the species was detected on the first visit, undetected on the second visit, and detected on the third visit. We can represent the probability of such a history as $\psi p(1 - p)p$, where ψ is the probability of occupancy and p is the probability of detection. This model-likelihood approach then can be extended to interannual parameters such as colonization (γ) and extinction (ε) (Fig. 1).

We used an information theoretic approach to model selection (Burnham and Anderson, 2002; Johnson and Omland, 2004). As recommended when the ratio between sample size and number of model parameters is less than 40, we derived the Akaike Information Criterion (AICc) for small samples (Burnham and Anderson, 2002) from the $-2\log$ -likelihoods ($-2LL$). AICc model weights then were derived and models ranked accordingly. Models with lowest AICc were considered most parsimonious, and pairs of models with an absolute difference in AICc of less than 2 were considered equally good (Burnham and Anderson, 2002). Because there is currently no adequate method for assessing absolute model fit when models include detection probability (MacKenzie et al., 2006, p. 109), our model selection procedure only could rank models and evaluate their relative fit.

We estimated single-visit detection probabilities for each of the ten species to examine the potential effects of detectability on inferences about its metapopulation dynamics and appropriate conservation planning for the species. We estimated detection probabilities of species by averaging across all models in which detection probabilities were not time-dependent (thus excluding models 5 and 7). Given species detection probability, we then calculated the minimum number of visits necessary to be 95% confident that a species was absent from a site in a given time step as $N_{\min} = \log(0.05) / \log(1 - p)$, where p is the model-averaged detection probability (Pellet and Schmidt, 2005).

If colonization is indeed best modeled with connectivity as a patch-level covariate, it is reasonable to expect that model

fit will be higher when the value for connectivity is calculated with the true mean dispersal distance for the species. Because this value was either unknown or imprecise, we created for each species a new set of models based on the best model that included connectivity as a covariate (model 9, 12, or 13). Ten new connectivity models, each with different dispersal distances (from 0.2 to 2 km in 0.2 km increments for butterflies and amphibians, and from 2 to 20 km in 2 km increments for birds), were calculated for each species. Using the model selection procedure described above, we calculated model weights. We assumed that higher model weights (and their associated estimates of dispersal distance) more accurately reflected the true ability of the species to disperse and to recolonize patches.

3. Results

For every species, changes in metapopulation occupancy among years were represented best by models with patch-specific extinction probabilities, colonization probabilities, or both (Table 3). Averaged across species, the best model included population size as a covariate of extinction probability, with all other parameters constant. The second-best model included population size as a covariate of extinction probability and connectivity as a covariate of colonization probability. The performance of the simplest model, in which probabilities of colonization, extinction, and single-visit detection were assumed to be constant, ranked third when averaged across all species (Table 4).

For all species of butterflies and amphibians, the two models that included population size as a covariate of extinction probability (models 11 and 13, negative correlation) accounted for more than 94% of the summed weights of all models, performing much better than patch area as a covariate in predicting extinction rates. For all six species of birds, models that included population size as a covariate predicted extinction rate equally well or better than models that included patch area as a covariate (Table 3). Correlations between patch area and population size were variable across species and taxonomic groups, ranging from 0.07 for the bird *P. villosus* and 0.15 for the butterfly *S. nokomis*, to 0.79 and 0.87 for the birds *D. petechia* and *M. melodia*, respectively.

Predictions of colonization probability were improved by including connectivity (positively correlated with probability of colonization) as a patch covariate for only 3 of 10 species (the butterfly *M. nausithous* and the birds *M. melodia* and *P. amoena*). For the other species, the ΔAICc between model 9 (constant probability of extinction and single-visit detection, connectivity covaries with probability of colonization) and model 1 (constant probability of extinction, detection, and colonization) was less than 2, indicating that patch-level connectivity conferred little advantage in predicting colonization events compared with models in which colonization probability was assumed to be constant.

For most species, modifying mean dispersal distance ($1/x$) in the best model changed the model likelihood only slightly (Fig. 2). For both species of butterflies, however, we identified a clear relationship between dispersal distance and model fit. For *M. nausithous*, the best model of colonization included a

mean dispersal distance of 1400 m, whereas for *S. nokomis*, both relatively short (200 m) and long (>2000 m) dispersal distances were strongly associated with probability of colonization (Fig. 2). For both amphibians, but especially *B. calamita*, dispersal distance was inversely correlated with model fit, indicating stronger support for short range dispersal (<400 m). We did not detect a clear correlation between dispersal distance and model fit for birds; for all six species, the 10 models had similar weights.

In general, model selection indicated that probabilities of extinction and colonization were better explained by models that included constant probabilities of detection than by models that included time-dependent probabilities of detection (models 5–8 in Table 4). These results suggest that, as we had believed, survey intensity for all species was roughly constant during the monitoring periods that informed our analyses. Single-visit detection probabilities were imperfect for all species, ranging from 23% likelihood of detection (*P. villosus*) to 81% (*D. petechia* and *M. melodia*). Mean detection probabilities within taxonomic groups were 60% for butterflies, 56% for amphibians, and 66% for birds. For three species, *M. nausithous*, *B. calamita*, and *P. villosus*, annual survey efforts were insufficient to provide 95% confidence that the species was absent from a given patch in any given year, suggesting that use of occupancy models allowing for imperfect detectability was especially appropriate to describe the metapopulation dynamics of these species (Table 5).

4. Discussion

Although our set of 10 species covered a wide range of life histories and ecological requirements, we obtained consistent results about the best predictors of changes in metapopulation occupancy among years. Overall, our best models included patch-specific extinction probabilities and, to a lesser extent, patch-specific colonization probabilities rather than probabilities that were constant or time-dependent. Our analyses suggest that the cost of obtaining a measure of population size for patch is worthwhile in terms of increasing ability to predict occupancy patterns over time. At least some measures of connectivity, however, may not improve the accuracy of predictions relative to models that assume a constant probability of colonization. An important caveat is that models including time-dependent parameters were heavily penalized in the model selection process (computation of the AICc) because they included a large number of parameters. Accordingly, selection of the most parsimonious model may serve to mask time-dependent patterns.

Extinction probabilities for eight species were better modeled as a function of population size than as a function of patch area. This may reflect the fact that population size and extinction probability usually are correlated negatively due to environmental and demographic stochasticity (Boyce, 1992; Inchausti and Halley, 2003). We would expect patch area to predict extinction rates equally well or better than population size if patch area reflected carrying capacity. For most of our species, however, the correlation between population size and patch area was weak. Use of patch area as a surrogate for population size is appealing because patch area is more easily

Table 3 – Model selection according to AICc for each species

Species	Model	Model	–2LL	n	K	AICc	w
<i>Speyeria nokomis</i>	11	$\psi(\text{year1});(\cdot)\varepsilon(\text{population size})p(\cdot)$	964.6	39	5	976.5	0.70
	13	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{population size})p(\cdot)$	963.5	39	6	978.2	0.30
	5	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(t)$	973.4	39	7	991.0	0.00
	10	$\psi(\text{year1});(\cdot)\varepsilon(\text{patch area})p(\cdot)$	981.5	39	5	993.3	0.00
	1	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(\cdot)$	984.3	39	4	993.4	0.00
	9	$\psi(\text{year1});(\text{connectivity})\varepsilon(\cdot)p(\cdot)$	984.1	39	5	995.9	0.00
	12	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{patch area})p(\cdot)$	981.3	39	6	996.0	0.00
	3	$\psi(\text{year1});(\cdot)\varepsilon(t)p(\cdot)$	982.2	39	6	996.8	0.00
	6	$\psi(\text{year1});(t)\varepsilon(\cdot)p(t)$	973.2	39	9	997.4	0.00
	7	$\psi(\text{year1});(\cdot)\varepsilon(t)p(t)$	973.3	39	9	997.5	0.00
	2	$\psi(\text{year1});(t)\varepsilon(\cdot)p(\cdot)$	984.1	39	6	998.7	0.00
	4	$\psi(\text{year1});(t)\varepsilon(t)p(\cdot)$	981.7	39	8	1002.5	0.00
	8	$\psi(\text{year1});(t)\varepsilon(t)p(t)$	973.1	39	11	1004.9	0.00
<i>Maculinea nausithous</i>	13	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{population size})p(\cdot)$	297.6	15	6	320.1	0.80
	11	$\psi(\text{year1});(\cdot)\varepsilon(\text{population size})p(\cdot)$	306.9	15	5	323.6	0.14
	5	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(t)$	295.2	15	7	325.2	0.06
	9	$\psi(\text{year1});(\text{connectivity})\varepsilon(\cdot)p(\cdot)$	323.0	15	5	339.7	0.00
	7	$\psi(\text{year1});(\cdot)\varepsilon(t)p(t)$	285.7	15	9	339.7	0.00
	1	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(\cdot)$	328.0	15	4	340.0	0.00
	12	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{patch area})p(\cdot)$	318.1	15	6	340.6	0.00
	6	$\psi(\text{year1});(t)\varepsilon(\cdot)p(t)$	288.1	15	9	342.1	0.00
	2	$\psi(\text{year1});(t)\varepsilon(\cdot)p(\cdot)$	322.3	15	6	344.8	0.00
	3	$\psi(\text{year1});(\cdot)\varepsilon(t)p(\cdot)$	329.8	15	6	352.3	0.00
	4	$\psi(\text{year1});(t)\varepsilon(t)p(\cdot)$	342.2	15	8	382.2	0.00
	8	$\psi(\text{year1});(t)\varepsilon(t)p(t)$	279.2	15	11	389.2	0.00
	10	$\psi(\text{year1});(\cdot)\varepsilon(\text{patch area})p(\cdot)$	373.2	15	5	389.9	0.00
<i>Bufo calamita</i>	11	$\psi(\text{year1});(\cdot)\varepsilon(\text{population size})p(\cdot)$	368.7	27	5	381.5	0.82
	13	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{population size})p(\cdot)$	368.4	27	6	384.6	0.17
	10	$\psi(\text{year1});(\cdot)\varepsilon(\text{patch area})p(\cdot)$	382.1	27	5	395.0	0.00
	1	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(\cdot)$	386.2	27	4	396.0	0.00
	12	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{patch area})p(\cdot)$	381.6	27	6	397.8	0.00
	9	$\psi(\text{year1});(\text{connectivity})\varepsilon(\cdot)p(\cdot)$	385.9	27	5	398.7	0.00
	2	$\psi(\text{year1});(t)\varepsilon(\cdot)p(\cdot)$	383.9	27	6	400.1	0.00
	3	$\psi(\text{year1});(\cdot)\varepsilon(t)p(\cdot)$	386.1	27	6	402.3	0.00
	5	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(t)$	385.9	27	7	405.8	0.00
	4	$\psi(\text{year1});(t)\varepsilon(t)p(\cdot)$	383.7	27	8	407.7	0.00
	6	$\psi(\text{year1});(t)\varepsilon(\cdot)p(t)$	383.4	27	9	412.0	0.00
	7	$\psi(\text{year1});(\cdot)\varepsilon(t)p(t)$	385.8	27	9	414.4	0.00
	8	$\psi(\text{year1});(t)\varepsilon(t)p(t)$	382.8	27	11	422.4	0.00
<i>Hyla arborea</i>	11	$\psi(\text{year1});(\cdot)\varepsilon(\text{population size})p(\cdot)$	427.0	27	5	439.9	0.82
	13	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{population size})p(\cdot)$	426.7	27	6	442.9	0.18
	1	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(\cdot)$	451.0	27	4	460.8	0.00
	9	$\psi(\text{year1});(\text{connectivity})\varepsilon(\cdot)p(\cdot)$	450.3	27	5	463.2	0.00
	10	$\psi(\text{year1});(\cdot)\varepsilon(\text{patch area})p(\cdot)$	451.0	27	5	463.9	0.00
	3	$\psi(\text{year1});(\cdot)\varepsilon(t)p(\cdot)$	448.7	27	6	464.9	0.00
	2	$\psi(\text{year1});(t)\varepsilon(\cdot)p(\cdot)$	450.3	27	6	466.5	0.00
	12	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{patch area})p(\cdot)$	450.3	27	6	466.5	0.00
	5	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(t)$	449.4	27	7	469.3	0.00
	4	$\psi(\text{year1});(t)\varepsilon(t)p(\cdot)$	448.1	27	8	472.1	0.00
	7	$\psi(\text{year1});(\cdot)\varepsilon(t)p(t)$	446.9	27	9	475.5	0.00
	6	$\psi(\text{year1});(t)\varepsilon(\cdot)p(t)$	448.8	27	9	477.4	0.00
	8	$\psi(\text{year1});(t)\varepsilon(t)p(t)$	446.4	27	11	486.0	0.00
<i>Selasphorus platycercus</i>	11	$\psi(\text{year1});(\cdot)\varepsilon(\text{population size})p(\cdot)$	134.4	12	5	154.4	0.87
	10	$\psi(\text{year1});(\cdot)\varepsilon(\text{patch area})p(\cdot)$	138.3	12	5	158.3	0.12
	1	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(\cdot)$	153.3	12	4	167.0	0.00
	12	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{patch area})p(\cdot)$	138.3	12	6	167.1	0.00
	2	$\psi(\text{year1});(t)\varepsilon(\cdot)p(\cdot)$	142.6	12	6	171.4	0.00
	9	$\psi(\text{year1});(\text{connectivity})\varepsilon(\cdot)p(\cdot)$	153.3	12	5	173.3	0.00
	3	$\psi(\text{year1});(\cdot)\varepsilon(t)p(\cdot)$	149.6	12	6	178.4	0.00
	13	$\psi(\text{year1});(\text{connectivity})\varepsilon(\text{population size})p(\cdot)$	149.8	12	6	178.6	0.00
	5	$\psi(\text{year1});(\cdot)\varepsilon(\cdot)p(t)$	152.6	12	7	194.6	0.00
	4	$\psi(\text{year1});(t)\varepsilon(t)p(\cdot)$	139.0	12	8	203.0	0.00

(continued on next page)

Table 3 – continued

Species	Model	Model	–2LL	n	K	AICc	w
	6	$\psi(\text{year1});(t)\epsilon(.)p(t.)$	141.8	12	9	249.8	0.00
	7	$\psi(\text{year1});(.)\epsilon(t)p(t.)$	148.8	12	9	256.8	0.00
<i>Picoides villosus</i>	11	$\psi(\text{year1});(.)\epsilon(\text{population size})p(..)$	84.9	12	5	104.9	0.76
	1	$\psi(\text{year1});(.)\epsilon(.)p(..)$	94.4	12	4	108.1	0.15
	9	$\psi(\text{year1});(\text{connectivity})\epsilon(.)p(..)$	91.0	12	5	111.0	0.04
	10	$\psi(\text{year1});(.)\epsilon(\text{patch area})p(..)$	91.5	12	5	111.5	0.03
	13	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{population size})p(..)$	83.6	12	6	112.4	0.02
	12	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{patch area})p(..)$	91.5	12	6	120.3	0.00
	2	$\psi(\text{year1});(t)\epsilon(.)p(..)$	91.9	12	6	120.7	0.00
	3	$\psi(\text{year1});(.)\epsilon(t)p(..)$	93.4	12	6	122.2	0.00
	5	$\psi(\text{year1});(.)\epsilon(.)p(t.)$	92.3	12	7	134.3	0.00
	4	$\psi(\text{year1});(t)\epsilon(t)p(..)$	95.2	12	8	159.2	0.00
	7	$\psi(\text{year1});(.)\epsilon(t)p(t.)$	91.1	12	9	199.1	0.00
	6	$\psi(\text{year1});(t)\epsilon(.)p(t.)$	95.4	12	9	203.4	0.00
<i>Troglodytes aedon</i>	10	$\psi(\text{year1});(.)\epsilon(\text{patch area})p(..)$	93.7	12	5	113.7	0.43
	11	$\psi(\text{year1});(.)\epsilon(\text{population size})p(..)$	93.7	12	5	113.7	0.43
	13	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{population size})p(..)$	88.2	12	6	117.0	0.08
	1	$\psi(\text{year1});(.)\epsilon(.)p(..)$	104.9	12	4	118.6	0.04
	9	$\psi(\text{year1});(\text{connectivity})\epsilon(.)p(..)$	99.2	12	5	119.2	0.03
	3	$\psi(\text{year1});(.)\epsilon(t)p(..)$	101.6	12	6	130.4	0.00
	12	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{patch area})p(..)$	103.2	12	6	132.0	0.00
	2	$\psi(\text{year1});(t)\epsilon(.)p(..)$	104.3	12	6	133.1	0.00
	5	$\psi(\text{year1});(.)\epsilon(.)p(t.)$	101.7	12	7	143.7	0.00
	4	$\psi(\text{year1});(t)\epsilon(t)p(..)$	100.9	12	8	164.9	0.00
	7	$\psi(\text{year1});(.)\epsilon(t)p(t.)$	99.2	12	9	207.2	0.00
	6	$\psi(\text{year1});(t)\epsilon(.)p(t.)$	101.1	12	9	209.1	0.00
<i>Dendroica petechia</i>	10	$\psi(\text{year1});(.)\epsilon(\text{patch area})p(..)$	93.8	12	5	113.8	0.49
	11	$\psi(\text{year1});(.)\epsilon(\text{population size})p(..)$	93.8	12	5	113.8	0.49
	12	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{patch area})p(..)$	92.7	12	6	121.5	0.01
	13	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{population size})p(..)$	92.7	12	6	121.5	0.01
	1	$\psi(\text{year1});(.)\epsilon(.)p(..)$	116.7	12	4	130.5	0.00
	9	$\psi(\text{year1});(\text{connectivity})\epsilon(.)p(..)$	115.3	12	5	135.3	0.00
	2	$\psi(\text{year1});(t)\epsilon(.)p(..)$	111.1	12	6	139.9	0.00
	3	$\psi(\text{year1});(.)\epsilon(t)p(..)$	113.0	12	6	141.8	0.00
	5	$\psi(\text{year1});(.)\epsilon(.)p(t.)$	110.9	12	7	152.9	0.00
	4	$\psi(\text{year1});(t)\epsilon(t)p(..)$	107.4	12	8	171.4	0.00
	6	$\psi(\text{year1});(t)\epsilon(.)p(t.)$	105.2	12	9	213.2	0.00
	7	$\psi(\text{year1});(.)\epsilon(t)p(t.)$	107.1	12	9	215.1	0.00
<i>Melospiza melodia</i>	9	$\psi(\text{year1});(\text{connectivity})\epsilon(.)p(..)$	112.7	12	5	132.7	0.46
	1	$\psi(\text{year1});(.)\epsilon(.)p(..)$	119.4	12	4	133.1	0.38
	11	$\psi(\text{year1});(.)\epsilon(\text{population size})p(..)$	116.0	12	5	136.0	0.09
	10	$\psi(\text{year1});(.)\epsilon(\text{patch area})p(..)$	117.4	12	5	137.4	0.04
	13	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{population size})p(..)$	109.5	12	6	138.3	0.03
	3	$\psi(\text{year1});(.)\epsilon(t)p(..)$	113.5	12	6	142.3	0.00
	2	$\psi(\text{year1});(t)\epsilon(.)p(..)$	116.1	12	6	144.9	0.00
	5	$\psi(\text{year1});(.)\epsilon(.)p(t.)$	106.7	12	7	148.7	0.00
	12	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{patch area})p(..)$	124.1	12	6	152.9	0.00
	4	$\psi(\text{year1});(t)\epsilon(t)p(..)$	110.0	12	8	174.0	0.00
	7	$\psi(\text{year1});(.)\epsilon(t)p(t.)$	104.7	12	9	212.7	0.00
	6	$\psi(\text{year1});(t)\epsilon(.)p(t.)$	105.6	12	9	213.6	0.00
<i>Passerina amoena</i>	13	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{population size})p(..)$	91.2	12	6	120.0	0.70
	9	$\psi(\text{year1});(\text{connectivity})\epsilon(.)p(..)$	101.9	12	5	121.9	0.27
	12	$\psi(\text{year1});(\text{connectivity})\epsilon(\text{patch area})p(..)$	98.2	12	6	127.0	0.02
	11	$\psi(\text{year1});(.)\epsilon(\text{population size})p(..)$	109.0	12	5	129.0	0.01
	10	$\psi(\text{year1});(.)\epsilon(\text{patch area})p(..)$	109.8	12	5	129.8	0.01
	1	$\psi(\text{year1});(.)\epsilon(.)p(..)$	119.9	12	4	133.6	0.00
	3	$\psi(\text{year1});(.)\epsilon(t)p(..)$	118.2	12	6	147.0	0.00
	2	$\psi(\text{year1});(t)\epsilon(.)p(..)$	119.0	12	6	147.8	0.00
	5	$\psi(\text{year1});(.)\epsilon(.)p(t.)$	110.4	12	7	152.4	0.00
	4	$\psi(\text{year1});(t)\epsilon(t)p(..)$	117.2	12	8	181.2	0.00

Table 3 – continued

Species	Model	Model	–2LL	n	K	AICc	w
	6	$\psi(\text{year1})\gamma(t)\epsilon(\cdot)p(t)$	109.2	12	9	217.2	0.00
	7	$\psi(\text{year1})\gamma(\cdot)\epsilon(t)p(t)$	109.3	12	9	217.3	0.00

–2LL is the –2log-likelihood of the model, n the sample size (number of patches), K the number of parameters included in the model, and w is the Akaike weight of the model. The sum of all model weights in a set of candidate models is 1. The higher the weight, the more parsimonious the model. Sample size for bird data did not allow computation of the most highly parameterized model [model 8, $\psi(\text{year1})\gamma(t)\epsilon(t)p(t)$], which had 11 parameters.

measured in the field (Moilanen, 2002), but our results do not support the use of patch area as a surrogate of population size. We acknowledge that our estimates of population size likely were biased to some extent because our estimates were based on counts rather than on field methods that account for imperfect detection of individuals (e.g., distance sampling or capture–recapture). We also recognize that not only average population size but temporal variance in population size might influence probability of extinction.

In most cases, adding connectivity as a patch-specific covariate did not improve predictions of colonization; a constant colonization probability was equally effective. We suspect this is because the underlying assumptions of our metric of connectivity – a widely used metric (Hanski, 1999) – are unlikely to match real life situations. That metric included distances between patches, population size, and mean dispersal distance (estimated from mark-recapture data). We did not attempt to estimate the ability of the species to use the matrix separating patches of habitat and density-independent movements among patches, both of which often affect dispersal rates. Other measures of connectivity, such as distance to closest neighboring patch or population, or sizes of individual populations within a given radius from each patch, also may be good fits to empirical data (Schmidt and Pellet, 2005). In addition, there is considerable evidence that patch quality affects colonization and extinction in taxonomic groups including butterflies (Dennis and Eales, 1999; Fleishman et al., 2002), amphibians (Sjögren-Gulve and Ray,

1996; Pope et al., 2000; Vos et al., 2000), birds (Erwin et al., 1998), and mammals (Pita et al., 2007). This may be especially true for relatively mobile species, such as migratory birds that return to the same patch networks every year. We did not attempt to quantify or include habitat quality in our models because our purpose was not to evaluate the relative importance of patch geometry and habitat quality, but to evaluate whether area, population size, and isolation were more effective predictors of patch occupancy than constant or time-dependent parameters.

Although connectivity did not improve predictions of colonization rates compared to a constant colonization probability, we identified an effect of dispersal distance on model weight for butterflies and amphibians. For the butterfly *M. nausithous*, we found a bell-shaped effect of dispersal distance on model weight, indicating that colonization data were best explained by intermediate-range dispersal (~1400 m); this distance was larger than reported in the literature (Nowicki et al., 2005). The discrepancy might indicate that individuals residing in our patch network, where the mean distance to the closest patch is 1.8 km, must travel longer distances to colonize a patch. For *S. nokomis*, by contrast, we found an apparent bimodal effect of dispersal distance. This likely reflects that in the metapopulation we studied, the distance among separate canyons typically is much greater than the distance among patches of habitat within an individual canyon (Table 1), and the uplands between canyons present topographic and ecological barriers to dispersal. It appeared that the amphibians in our analyses (*B. calamita* and *H. arborea*) need not disperse relatively far in order to recolonize the ponds that serve as their habitat, which is consistent with previous work by Schmidt and Pellet (2005). The effect was extremely strong for *B. calamita*.

For birds, however, we did not detect a strong relationship between dispersal distances and colonization rates. All species included in our analyses, with the exception of *P. villosus* (a resident of the Great Basin), are migrants that can travel hundreds of kilometers between nesting and wintering habitats. When these species return to breed in the Great Basin, their probability of colonizing a patch that was vacant the previous year may depend less on the location of the patch or its isolation from other patches than on factors that we did not include in our analyses, such as total habitat area within a given region and habitat quality.

If survey intensity is inadequate to detect all true presences, false absences erroneously may be interpreted as extirpations. As a result, use of presence/absence data to examine metapopulation dynamics may overestimate both extinction rates and colonization rates. Our monitoring protocols

Table 4 – Mean ranks for each model, averaged across all species

	Model	Mean model rank (SD)
11	$\psi(\text{year1})\gamma(\cdot)\epsilon(\text{population size})p(\cdot)$	1.8 (1.0)
13	$\psi(\text{year1})\gamma(\text{connectivity})\epsilon(\text{population size})p(\cdot)$	3.3 (2.2)
1	$\psi(\text{year1})\gamma(\cdot)\epsilon(\cdot)p(\cdot)$	4.0 (1.5)
10	$\psi(\text{year1})\gamma(\cdot)\epsilon(\text{patch area})p(\cdot)$	4.2 (3.4)
9	$\psi(\text{year1})\gamma(\text{connectivity})\epsilon(\cdot)p(\cdot)$	4.3 (1.8)
12	$\psi(\text{year1})\gamma(\text{connectivity})\epsilon(\text{patch area})p(\cdot)$	5.9 (2.1)
3	$\psi(\text{year1})\gamma(\cdot)\epsilon(t)p(\cdot)$	7.4 (1.3)
2	$\psi(\text{year1})\gamma(t)\epsilon(\cdot)p(\cdot)$	7.6 (1.6)
5	$\psi(\text{year1})\gamma(\cdot)\epsilon(t)p(t)$	7.7 (2.5)
4	$\psi(\text{year1})\gamma(t)\epsilon(t)p(\cdot)$	10.3 (0.7)
7	$\psi(\text{year1})\gamma(\cdot)\epsilon(t)p(t)$	10.7 (2.1)
6	$\psi(\text{year1})\gamma(t)\epsilon(\cdot)p(t)$	10.9 (1.4)
8	$\psi(\text{year1})\gamma(t)\epsilon(t)p(t)$	12.8 (0.5)

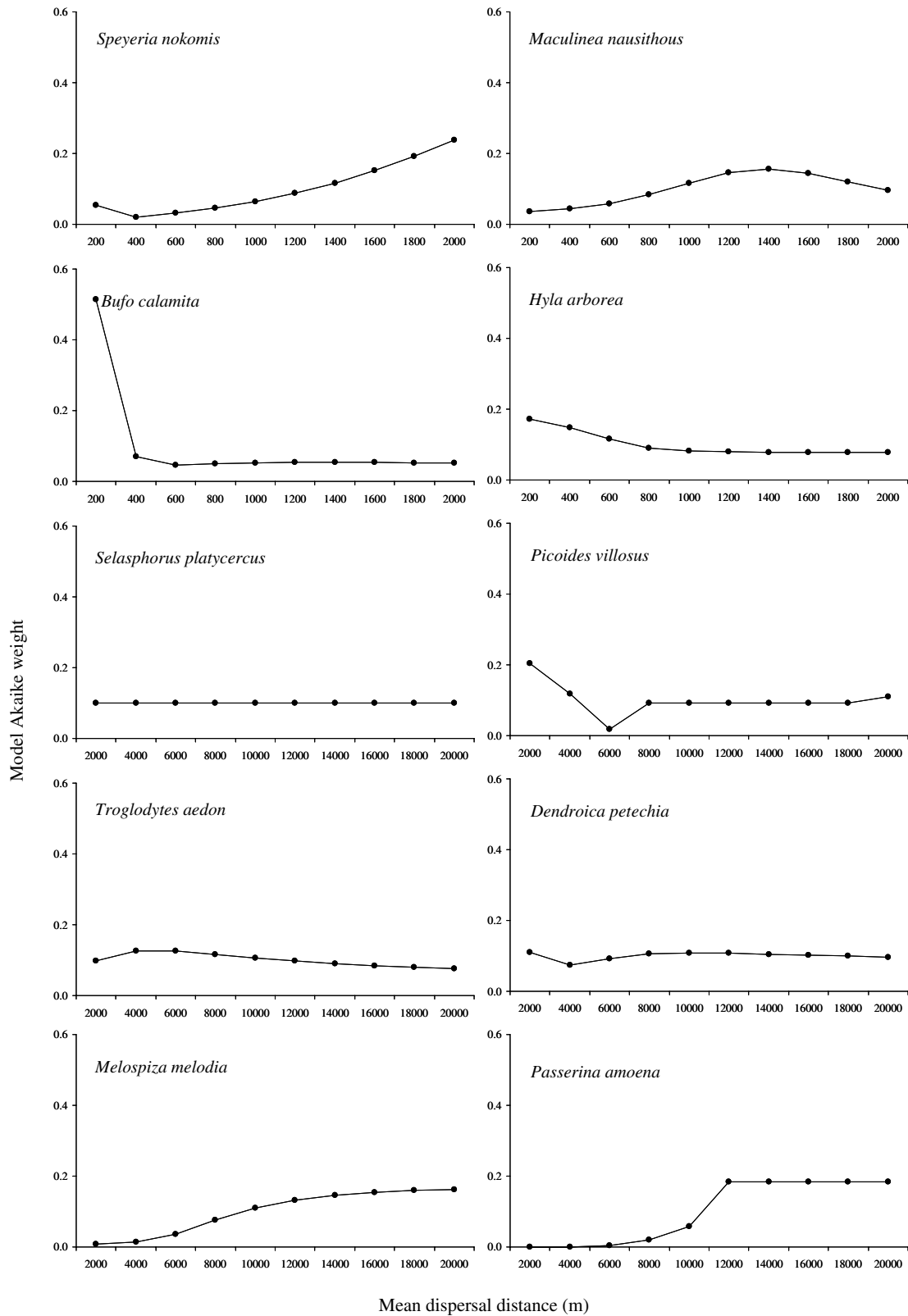


Fig. 2 – Model weight as a function of dispersal distance in the best model that included connectivity as a covariate of probability of colonization.

generally were adequate to determine patch occupancy. For one species in each of the three taxonomic groups, however, survey intensity was insufficient to detect absences in a given

year correctly. This emphasizes the difficulty of designing a protocol to survey multiple species simultaneously and accurately (Pellet and Schmidt, 2005).

Table 5 – Single-visit detection probability, sampling effort required to avoid false absences (95% certainty), and actual sampling effort for each species

Species	Detection probability (%)	Required number of visits per site per year	Mean number of visits per year (SD)	Sufficient sampling effort?
<i>Speyeria nokomis</i>	45	5	5.3 (1.1)	Yes
<i>Maculinea nausithous</i>	75	3	2.3 (0.8)	No
<i>Bufo calamita</i>	43	6	3.6 (1.9)	No
<i>Hyla arborea</i>	70	3	3.6 (1.9)	Yes
<i>Selasphorus platycercus</i>	66	3	3.0 (0.0)	Yes
<i>Picoides villosus</i>	23	12	3.0 (0.0)	No
<i>Troglodytes aedon</i>	75	3	3.0 (0.0)	Yes
<i>Dendroica petechia</i>	81	2	3.0 (0.0)	Yes
<i>Melospiza melodia</i>	81	2	3.0 (0.0)	Yes
<i>Passerina amoena</i>	71	3	3.0 (0.0)	Yes

The butterfly *M. nausithous* was relatively easy to detect (75% detection probability per visit if present), but absences may not have been recorded because the number of visits was low. Detectability was lower for *S. nokomis* (45%), but the number of visits per patch was sufficient to be 95% confident that apparent patch-level absences were true absences. The low detection probability for this species may reflect staggered emergence (up to several weeks) among patches in which microclimates are different, or the typically cryptic movements of females.

Average detection probabilities across all years for amphibians were variable. Because *H. arborea* had a detection probability of 70% on each visit, the monitoring protocol was sufficient to detect true absences each year with 95% confidence. *B. calamita*, however, has a somewhat more discrete calling behavior (Pellet and Schmidt, 2005), and therefore was less likely to be detected when present (43%). Its true distribution may not have been identified correctly during our surveys. These results are concordant with Pellet and Schmidt (2005) and support the use of occupancy models that allow for imperfect detection probabilities when estimating both occupancy and turnover. Our work thus demonstrates that imperfect detection of occupancy patterns can lead to erroneous inferences.

Three surveys are considered sufficient to determine which species of birds are present at point count locations (Buckland et al., 2001; Siegel et al., 2001); in our work, species accumulation curves for birds at multiple spatial scales generally approached an asymptote before the third round of surveys (Betrus, 2002). Detection probabilities for birds were above 66% for all but one species, *P. villosus* (23%). This low value may be due to the fact that this woodpecker rarely uses territorial vocalization and primarily is detected when drumming, a behavior that is less frequent than is vocalization in our other study species. Again, although our monitoring protocol appears adequate to detect most species accurately, it may not be sufficient to detect all species.

As other workers have suggested (Singer and Thomas, 1996; Thomas et al., 1996; Boughton, 1999), the solid mathematical framework that has been the foundation of metapopulation theory should be expanded to account for parameters other than patch size and location. Our data suggest that area often is an inadequate surrogate measure of population size,

therefore is less effective than population size for predicting extinction of patches in a metapopulation. Our work indicates that when possible, monitoring protocols intended to track metapopulation dynamics should include a measure of population size in addition to patch area. We also found that the traditional metric for isolation (connectivity) did not perform well in predicting probabilities of patch colonization. This finding adds further support for the recommendation that, in most cases, other parameters (most appropriately, habitat quality parameters) should be measured and included in metapopulation models whenever feasible to predict adequately long-term persistence of species of conservation concern. For most if not all taxonomic groups, conservation planners should be aware of the potential limitations of metapopulation models that are based only on patch area and isolation.

Acknowledgements

Thanks to D.A. Saunders and two anonymous reviewers for comments that improved the manuscript. This work was funded by the Swiss National Science Foundation postdoctoral grant PBLAA-109803, Center for Conservation Biology at Stanford University, Nevada Biodiversity Research and Conservation Initiative, and the Joint Fire Science Program via the Rocky Mountain Research Station, US Department of Agriculture Forest Service.

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