Comparison of Two Types of Metapopulation Models in Real and Artificial Landscapes

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Abstract: Application of metapopulation models is becoming increasingly widespread in the conservation of species in fragmented landscapes. We provide one of the first detailed comparisons of two of the most common modeling techniques, incidence function models and stage-based matrix models, and test their accuracy in predicting patch occupancy for a real metapopulation. We measured patch occupancies and demographic rates for regional populations of the Florida scrub lizard (Sceloporus woodi) and compared the observed occupancies with those predicted by each model. Both modeling strategies predicted patch occupancies with good accuracy (77–80%) and gave similar results when we compared hypothetical management scenarios involving removal of key habitat patches and degradation of habitat quality. To compare the two modeling approaches over a broader set of conditions, we simulated metapopulation dynamics for 150 artificial landscapes composed of equal-sized patches (2–1024 ha) spaced at equal distances (50–750 m). Differences in predicted patch occupancy were small to moderate (<20%) for about 74% of all simulations, but 22% of the landscapes had differences of >50%. Incidence function models and stage-based matrix models differ in their approaches, assumptions, and requirements for empirical data, and our findings provide evidence that the two models can produce different results. We encourage researchers to use both techniques and further examine potential differences in model output. The feasibility of obtaining data for population modeling varies widely among species and limits the modeling approaches appropriate for each species. Understanding different modeling approaches will become increasingly important as conservation programs undertake the challenge of managing for multiple species in a landscape context.

Comparación de Dos Tipos de Modelos de Metapoblaciones en Paisajes Reales y Artificiales

Resumen: Cada vez es mayor la aplicación de modelos de metapoblaciones para la conservación de especies en paisajes fragmentados. Proporcionamos una de las primeras comparaciones detalladas de dos de las técnicas más comunes para modelar, los modelos de función de incidencia y los modelos demográficos basados en etapas, y probar su precisión en una metapoblación real. Medimos la tasa de ocupación de fragmentos y las tasas demográficas de poblaciones regionales de la lagartija Sceloporus woodi y comparamos la ocupación observada con la predicha por cada modelo. Ambas estrategias de modelaje predijeron la ocupación de fragmentos con buena precisión (77–80%) y dieron resultados similares cuando comparamos escenarios de manejo hipotéticos que involucraban la remoción de fragmentos de hábitat claves y la degradación de la calidad del hábitat. Para comparar las dos aproximaciones al modelaje en un conjunto de condiciones más amplio, simulamos la dinámica metapoblacional en 150 paisajes artificiales compuestos de fragmentos del mismo tamaño (2–1024 ha) separadas por la misma distancia (50–750 m). Las diferencias en la ocupación de fragmentos predicha fueron pequeñas a moderadas (menos de 20%) en aproximadamente 74% de todas las simulaciones, pero 22% de los paisajes tenían diferencias que excedían el 50%. Modelos de función de incidencia y modelos de matriz debido a la naturaleza artificial de estos paisajes y la ausencia de datos de campo, consideramos que estos resultados proporcionan evidencia preventiva de que los dos modelos pueden producir resultados distintos. Discutimos como los modelos de función de incidencia y los modelos demográficos basados en etapas son distintos en sus aproximaciones, supuestos y requerimientos para datos empíricos, y sugerimos que los investigadores utilicen ambas técnicas y comparen resultados cuando sea posible. La
Introduction

How a species responds to the heterogeneous distribution of habitat and resources may strongly influence its long-term persistence (MacArthur & Wilson 1967; Levins 1969; Simberloff & Abele 1976; Soule 1987; Fahrig & Pal- oheim 1988; Gilpin & Hanski 1991). Whether a particular species is likely to persist in a given landscape is an important question from the standpoints of both theory and practice. Conservation biologists are increasingly relying on metapopulation models to address such questions (e.g., Hanks & Thomas 1994; LaHaye et al. 1994; Turner et al. 1995; Hanks et al. 1996; Wiens 1996; Hanski & Simberloff 1997).

A variety of metapopulation models are now available that differ greatly in data requirements and model assumptions (Hanski 1999). Two popular but different types of metapopulation models are the incidence function model (Hanski 1994) and stage-based matrix models such as Vortex, ALEX, and RAMAS (reviewed by Lindenmayer et al. 1995). Stage-based matrix models have been applied to a broad range of species; examples include the Snail Kite (Rostrhamus sociabilis; Beissinger 1995), Florida Scrub-Jay (Aphelocoma coeruleascens; Root 1998; Breining et al. 1999), Florida manatee (Trichechus manatus; Marmontel et al. 1997), and lower keys marsh rabbit (Sylvilagus palustris bejneri; Forys & Humphrey 1999). The weaknesses of stage-based matrix models have been reviewed by Beissinger and Westphal (1998) and Groom and Pascual (1998). Incidence function models have been developed for fewer species; examples include Florida scrub plants (Quintana-Ascencio & Menges 1996) and several species of butterflies (Hanski 1999). Because of the increasing popularity of the incidence function and stage-based matrix models, it is important for biologists to understand the substantial differences between these two approaches.

We provide one of the first detailed comparisons of incidence function and matrix approaches by modeling the metapopulation dynamics of the Florida scrub lizard (Sceloporus woodi) within a large study area with naturally occurring habitat patches. We examined the relative merits and limitations of the incidence function model and a stage-based matrix model by comparing their data requirements and assumptions and their predictive accuracy based on patch-occupancy data. We also compared predictions of the two models for different management scenarios within our study area by simulating degradation of habitat quality and removal of key habitat patches. To extend our comparison to other landscape configurations, we simulated a series of 150 artificial landscapes varying in patch size and isolation and evaluated the congruence of predicted patch occupancy for the two models.

Methods

Study Site, Species Biology, and Patch Data

We conducted our study at Avon Park Air Force Range (15 km east of Avon Park, Florida), which contains one of the largest remaining areas of scrub (2300 ha) in central Florida. Florida scrub is found on relic sand dunes of the central ridge of the Florida peninsula and in strands along more recent coastal sand dunes (Christman 1988; Fernald 1989; Meyers 1990). This unique system is naturally fragmented into an archipelago of habitat islands surrounded by more mesic and hydric habitats unsuitable for obligate scrub organisms. The scrub lizard is endemic to scrub habitat and some open sandhill habitats of south and central Florida (Jackson 1973a, 1973b; De-Marco 1992).

We visually delineated all scrub patches on Avon Park Air Force Range through soil, topographic, and vegetation maps and infrared aerial photographs (n = 95 patches). Boundaries of patches were drawn on aerial photos and digitized on scanned, georeferenced images of these photographs. To analyze the landscape at a spatial scale relevant to scrub lizards, we delineated regional clusters of patches likely to be isolated demographically from one another. Using a geographic information system (GIS), we generated dispersal buffers around each scrub patch that represented the estimated maximum dispersal distance of scrub lizards (750 m, Hokit et al. 1999) and grouped patches with overlapping buffers into clusters (Fig. 1). For each scrub patch in each cluster, we measured total area of the patch, percent cover of bare sandy habitat (a measure of habitat quality for scrub lizards; Hokit et al. 1999), and edge-to-edge distance to all other patches within the same cluster (for details of GIS procedures, see Branch et al. 1999; Hokit et al. 1999). To determine the presence or absence of scrub lizards, we conducted visual searches annually (1994–1998) in all scrub patches, and more often when no lizards were found (two to five times each year). Only two of the six
clusters (referred to as north and south clusters) contained scrub lizard populations, although habitat was adequate in other clusters (Hokit et al. 1999). In 1994 we found scrub lizards in 17 of the 33 patches in the south cluster and in 9 of 29 patches in the north cluster (Fig. 1). Between 1994 and 1998, we recorded two colonization events and six extinction events.

**Incidence Model**

**MODEL STRUCTURE**

The incidence function model, described in detail by Hanski (1994, 1999), relies on a “snapshot” of the presence or absence of a species in a set of habitat patches. The modeling objective is to estimate patch-specific colonization and extinction probabilities for a particular network (cluster) of patches and then use these estimates to make predictions about patch occupancy, transient dynamics, and regional population persistence. The primary assumptions of the Hanski model are that (1) the observed cluster of patches is in a dynamic equilibrium of colonization and extinction; (2) local (within-patch) demographic processes occur quickly relative to regional dynamics and may be ignored; (3) patch occupancy can be determined for discrete intervals (e.g., patches are either occupied or unoccupied for the unit time interval); (4) extinction ($E_j$) is a function of patch size; (5) colonization ($C_i$) is a function of the number of migrants and the propagule size required to establish a population; (6) within discrete time intervals, extinction occurs before colonization; (7) if $E_j$ and $C_i$ are relatively constant, then the probability of patch occupancy ($J_i$) equals $C_i / (C_i + E_i)$.

We modeled the patch-specific extinction probability ($E_i$) for scrub lizards as follows (Hanski 1994; Hanski et al. 1996):

$$E_i = \min[\mu/A_i^\kappa, 1],$$

where $A_i$ is the total area (ha) of patch $i$, $\mu$ is the probability that a population in a patch of unit size (e.g., 1 ha) will go extinct, and $\kappa$ is a coefficient describing the relationship between patch size and extinction probability. Because scrub lizards prefer open, sandy habitat, we replaced $A_i$ in equation 1 with the “effective area” ($A_i^\prime$) given by $Q_i A_i / Q^\prime_i$, where $Q_i$ is the percentage of open, sandy habitat estimated for patch $i$ and $Q^\prime_i$ is the percentage of open, sandy habitat for the patch with the highest proportion of bare, sandy habitat (Hanski 1994).

We assumed that patch-specific colonization probability ($C_i$) depends on the distance to other patches within the same cluster occupied by scrub lizards and on the respective areas of occupied patches (which are associated with population size and thus, presumably, with the number of potential migrants). Thus, $C_i$ is defined as

$$C_i = 1 / (1 + (y'/S_i)^2),$$

where $y'$ is a parameter that describes the colonization ability of the species and $S_i$ is a patch-specific isolation parameter defined as

$$S_i = \sum p_j \exp(-\alpha d_{ij}) A_j^\prime,$$

where $p_j = 0$ for unoccupied patches and 1 for occupied patches, $\alpha$ is a coefficient describing the relationship between migrant survival and migration distance, $d_{ij}$ is the distance (m) from patch $i$ to patch $j$, and $A_j^\prime$ is the effective area of patch $j$. To estimate coefficient $\alpha$, we used nonlinear regression to fit the equation $P = \exp(-\alpha d)$ to the observed proportion of occupied patches ($P$) as a function of distance ($d$) to the nearest occupied patch (Hokit et al. 1999). We then estimated the $S_i$ values using an analog program written in BASIC.

Following Hanski (1994), and provided that a particular regional population complies with the given assumptions, the patch-specific probability of occupancy ($J_i$) may be defined by the model

$$J_i = 1 / (1 + [y'/S_i^2] \mu/A_i^\kappa).$$

Alternatively, the patch-specific probability may be defined by

$$J_i = 1 / (1 + (\mu'/S_i^2 A_i^\kappa)).$$
where \( z \) is a constant that determines the shape of the function relating the number of migrants to the probability of successful colonization and \( \mu' \) is a composite variable described by \( \mu' = \mu y^2 \) (Hanski 1994). Equation 5 incorporates “rescue effects” in which local populations may go extinct but then be recolonized within any discrete time interval (Hanski 1994).

### PARAMETER ESTIMATION

To estimate patch-specific colonization and extinction probabilities, the unknown parameters in equation 1 (\( \mu \) and \( x \)) and equation 2 (\( y' \)) must be estimated by means of either equation 4 or 5. We fit both equations to the observed patch-occupancy data for scrub lizards. We replaced the unknown \( J_i \)'s by the observed occupancies (\( p_i \)'s) and, using maximum likelihood regression (Neter et al. 1989), we fit both equations to pooled data from the north and south clusters. To assess which equation (4 or 5) best fit the data, we compared the alternatives to a logistic regression model that included only \( A_i \) data. Patch area was positively associated with scrub lizard patch occupancy (\( p < 0.001 \)) in the logistic model. Lacking spatial information, however, the logistic regression model did not include effects due to patch location and provided a null model to compare with the alternative incidence function models (Hanski et al. 1996). We compared the models using likelihood ratio tests and estimates of the minimum negative log-likelihood function (Neter et al. 1989).

Both alternatives fit the data better than the logistic model (Table 1). Equations 4 and 5 could not be compared with likelihood ratio tests because of the lack of degrees of freedom. Equation 5 had a lower log-likelihood function, however, suggesting a better fit. Therefore, we used the parameter estimates from equation 5 in all subsequent analysis.

To estimate the extinction parameter \( \mu \), we first estimated \( y' \) using data on patch-occupancy turnover (colonization and extinction) from 5 years of observations and the equation described by Hanski (1994):

\[
T = \Sigma l / S_i^2 + y'^2 / S_i^2 \left( 1 - p_i / A_i \right) + \mu y^2 / A_i, \quad (6)
\]

where \( T \) is the total number of turnover events. Using equation 6, the total number of turnover events (8), patch data, and the estimates of \( \mu' \) (1.258) and \( y' \) (0.974), we numerically determined the value of \( y' \) (4.04) with a program written in BASIC. We then estimated the value of \( \mu \) (0.076) from \( \mu = \mu y^2 \) (Hanski 1994).

### Stage-Based Matrix Model

Our matrix model, developed with RAMAS/metapop (Akçakaya 1994), incorporated a stage-matrix approach for modeling local (within-patch) demography and a distance function for modeling migration rates between patches. Demographic and dispersal parameters were based on data from an extensive field study of scrub lizards that included mark-recapture on eight trapping grids (each 1 ha) sampled at 1-month intervals for 2 years (Branch et al. 1996). Our model assumptions were as follows: (1) a single sex (females) was modeled; (2) dispersal between patches was simulated with a simple distance-weighted function; (3) density dependence was modeled with a population ceiling; (4) demographic stochasticity of survival was modeled with a binomial function, stochasticity of fecundity with a poisson function, and environmental stochasticity with annual standard deviates (Akçakaya 1994); (5) potentially important factors for which no data exist were ignored (e.g., catastrophes, correlation of environmental stochasticity).

Because scrub lizards rarely survive more than 2 years (Hartmann 1995; Branch et al. 1996), we described local population demography using a three-stage matrix (Table 2). We defined stage 1 as occurring from the time of hatching (June-November) to the following May, the beginning of the lizards’ first reproductive season. Stages 2 and 3 occurred during the lizards’ first and second active reproductive seasons, respectively. Because we could not accurately age lizards after they reached 45 mm in snout-vent length (Jackson & Telford 1974; DeMarco 1992), we assumed that fecundity and survival rates were equivalent for these stages (Table 2). In other areas, females oviposite an average of four eggs per clutch and produce an average of three clutches per year (Jackson & Telford 1974). Egg mortality has not been examined for scrub lizards but has been estimated as 5–10% for other Sceloporus (e.g., Overall 1994). Based on these studies, we estimated that females in large patches successfully produce 11 hatchlings per reproductive season. Because recruitment in small patches (<7 ha) is 44% lower than recruitment in large patches (Branch et al. 1996), we estimated that females in small patches produce 6.16 hatchlings per reproductive season.

To estimate stage 1 survivorship, we calculated survivorship to the following May for each monthly cohort from June through November in small and large patches. We then averaged survivorship across the cohorts for both small and large patches (Table 2; Branch et al. 1999).

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**Table 1. Results of comparisons between alternative versions of the incidence function model and the simple logistic model for patch area.*

<table>
<thead>
<tr>
<th>Model</th>
<th>( n_p )</th>
<th>LF</th>
<th>Models compared</th>
<th>LRT</th>
<th>( \chi^2 )</th>
<th>df</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Equation 4</td>
<td>3</td>
<td>41.02</td>
<td>1 vs. 3</td>
<td>27.00</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>(2) Equation 5</td>
<td>3</td>
<td>34.14</td>
<td>2 vs. 3</td>
<td>40.76</td>
<td>1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>(3) Logistic model</td>
<td>2</td>
<td>54.52</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Abbreviations: \( n_p \), number of estimated parameters; LF, minimum value of the negative log-likelihood function; LRT, likelihood ratio chi-square statistic; df, degrees of freedom for LRT \( \chi^2 \).*
We estimated stage 2 and 3 survivorship rates by multiplying the monthly survivorship estimates (large patches, 0.83%; small patches, 0.79%; Branch et al. 1996) over a 12-month annual cycle (Table 2).

Because we lacked long-term data, we did not include the effects of catastrophes or correlations in environmental stochasticity among patches. We assumed that patches were at carrying capacity and lizards had a stable age distribution at the start of each simulation. We estimated the carrying capacity of each patch by multiplying the effective area by the average density estimate (54 lizards per ha for patches of <7 ha; 82 lizards per ha for patches of ≥7 ha) determined from mark-recapture studies (Branch et al. 1996). The mean individual growth rate of females is influenced by density (Branch et al. 1996). Therefore, we assumed that ceiling-type density dependence operates in all patches (Akçakaya 1994).

Our estimates for scrub lizard dispersal characteristics were speculative because there are no data on the dispersal rates of scrub lizards or of most other small-bodied lizards. Clobert et al. (1994) found that more than 50% of juvenile common lizards (Lacerta vivipara) dispersed farther than the size of one adult home range within a habitat patch, but they failed to document dispersal between habitat patches. Similarly, of more than 1300 scrub lizards captured on 1-ha sampling plots, we recaptured 10% of the lizards between 50 and 100 m from the edge of the sampling plots but did not document interpatch dispersal (Branch et al. 1996). For modeling purposes, we assumed that 10% of stage 1 lizards disperse from each occupied patch. Because adults have relatively stable home ranges (Branch et al. 1996), we assumed that only stage 1 individuals migrate between scrub patches and that migrants disperse among all patches within 750 m of the source patch. To provide distance-weighted estimates for the pairwise migration matrix in RAMAS/metapop, we used the function

\[ m_{ij} = \exp(-\alpha d_{ij}) (n_i/t) / N_i, \]

where \( m_{ij} \) is the annual proportion of migrants from patch \( i \) to patch \( j \), \( \alpha \) and \( d_{ij} \) are as in the incidence function models above, \( n_i \) is the total number of migrants from patch \( i \) (estimated as 10% of the juvenile population in patch \( i \) at carrying capacity), \( t \) is the number of patches within 750 m of patch \( i \), and \( N_i \) is the abundance of patch \( i \) at carrying capacity.

Assessment of the Accuracy of Models in Predicting Patch Occupancy

We simulated the transient dynamics of patch occupancy by scrub lizards in the north and south clusters of scrub patches (Fig. 1) with both models. We iterated the RAMAS model for 100 years, starting with all patches occupied, and for 100 replications. For the incidence function approach, we used an iterative program to generate stochastic extinction and colonization events by comparing randomly generated numbers with estimates (using equations 1 and 2) of the patch-specific extinction and colonization probabilities per unit time interval (1 year). We iterated the model for 1500 years, starting with all patches occupied and replicated this procedure for 100 simulations. The different time scales for the stage-based matrix model and incidence function model reflect differing rates of the two modeling techniques in reaching equilibrium. To assess the performance of the models, we (1) observed whether the models stabilized at an equilibrium value for the proportion of occupied patches, (2) compared model predictions for the proportion of occupied patches with the observed proportion of occupied patches in the field, and (3) compared the observed versus the predicted patch occupancy for specific patches using Fisher exact tests.

Model Sensitivity

We performed sensitivity analyses to assess how sensitive the models were to parameter estimates. In the incidence function model, the estimated parameters used in equations 1 and 2 were increased individually by 25%. In the stage-based matrix model, fecundity, survivorship, and migration parameters were increased individually by 25%. For each model, 100 replicate simulations of transient dynamics were performed for each parameter change to estimate the proportion of occupied patches. To obtain sensitivity values, we divided the percent change in the model output by the percent change in the input parameter.

Comparison of Simulated Management Scenarios

An important application of models in conservation is to understand the potential effects of environmental change. Using both models, we generated 50-year projections of the proportion of occupied patches for the north and south clusters of scrub patches under three scenarios. For scenario 1, we assumed that habitat quality would remain constant for the next 50 years. For scenario 2, we included a 6% decrease in habitat quality annually.

Table 2. Stage matrices for large and small (<7 ha) patches used to parameterize the matrix model.

<table>
<thead>
<tr>
<th></th>
<th>Large patch</th>
<th>Small patch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>stage 1 2 3</td>
<td>stage 1 2 3</td>
</tr>
<tr>
<td>Fecundity</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>6.16</td>
</tr>
<tr>
<td>Survivorship</td>
<td>0.18</td>
<td>0.00</td>
</tr>
<tr>
<td>Survivorship</td>
<td>0.12</td>
<td>0.06</td>
</tr>
<tr>
<td>Survivorship</td>
<td>0</td>
<td>0.06</td>
</tr>
<tr>
<td>Survivorship</td>
<td>0.06</td>
<td>0.06</td>
</tr>
</tbody>
</table>

\[ \text{Patch Occupancy} \]
over the 50-year interval to simulate the effects of fire suppression. Our estimate of change in habitat quality was based on estimates of the decrease in sandy habitat in scrub patches in the absence of burning from a sequence of aerial photographs of Avon Park Air Force Range over six decades (Branch et al. 1996). The decrease in habitat quality was modeled as a decrease in effective patch area in the incidence function model and as a linear decrease in carrying capacity in the stage-based matrix model. For scenario 3, we included an annual decrease in habitat quality and removed from the simulation two large patches from the south and one large patch from the north as if the patches had been eliminated from the landscape (Fig. 1). Because we assumed that initial abundance was at carrying capacity for all occupied patches, dynamics were highly variable for the first 40 years of simulations in the stage-based matrix model. We allowed this model to run for 90 years and then eliminated the first 40 years. Because of the arbitrary nature of this cut-off point, we could not directly compare the trajectories of the stage-based matrix model and the incidence function model. Our goal for this set of simulations was a qualitative comparison of the two models.

Comparison within Artificial Landscapes

To compare the two modeling approaches across a range of landscape configurations, we applied the models to artificial landscapes composed of 20 patches. All patches were of equal size and distance from one another, and we systematically varied patch size from 2 to 1024 ha at geometric increments (2, 4, 8, . . . ) and isolation from 50 to 750 m at 50-m increments. To simplify model setup, and following the assumption of Levins’ (1969) original metapopulation model, we assumed that all patches were the same distance from one another. For each simulation, we used the same parameters as in our natural landscape model and started with all patches occupied. We then modeled the transient dynamics of patch occupancy as described in the section on model accuracy. We repeated this simulation procedure for various area-by-isolation combinations and compared the proportion of patches predicted to be occupied by the incidence function model and the matrix model.

To assess how model parameters may contribute to differences between the two models, we conducted additional simulations for these two area-by-isolation combinations. We systematically manipulated each of the five parameters for the stage-based matrix model and repeated simulations in an attempt to achieve congruence with the incidence function model. We repeated this procedure for the four parameters of the incidence function model in an attempt to achieve congruence with the matrix model. Our purpose was not to complete a comprehensive analysis of all combinations of all parameters but rather to quickly assess whether congruence was possible and which parameter manipulations would potentially produce congruence. Inability to achieve congruence might indicate that differences were due to model structure rather than parameter values. If congruency could be achieved, we noted whether the altered parameter settings were plausible biologically. Differences between the two models might then be due to poor parameter estimates for one or both models.

Results

Comparison of Model Accuracy and Sensitivity in a Real Landscape

Both the incidence function and stage-based matrix models approached a steady state for the predicted proportion of occupied patches for both the south and north clusters of patches (Fig. 2). The incidence function model

Figure 2. Transient dynamics of estimated patch occupancy (±SD) by scrub lizards for the south cluster using (a) the incidence function model and (b) the stage-based demographic model. Transient dynamics of the north cluster (not shown) exhibited similar properties. Different time scales reflect different rates required to reach equilibrium for the two modeling techniques.
predicted 17 occupied patches for the south cluster and 11 occupied patches for the north cluster. The matrix model predicted 15 occupied patches for the south cluster and 11 occupied patches for the north cluster. Both models compared well with the observed patch-occupancy data. In most years, 17 patches were occupied in the south cluster and 9 patches were occupied in the north cluster.

Both models also did well in predicting patch occupancy for specific patches in the south and north clusters (all Fisher’s exact tests, \( p < 0.001 \)). The incidence function model correctly predicted patch occupancy for 73% of the patches in the south cluster, 83% of the patches in the north cluster, and 77% overall. The stage-based matrix model correctly predicted patch occupancy for 84% of the patches in the south cluster, 76% of the patches in the north cluster, and 80% overall. The two models agreed on 74% of the overall patch occupancies. Agreement was weakest for patches of 2–12 ha (Fig. 3). The six largest patches had areas of >12 ha and were always predicted to be occupied by both models.

The 23 smallest patches were <2 ha in area and were always predicted to be unoccupied except for 3 that were within 100 m of a large patch.

Both models are insensitive to changes of 25% for most parameter values (Table 3); the incidence function model was somewhat less sensitive than the stage-based matrix model. None of the sensitivity values for the incidence function model were above 1, indicating that the change in the model output was less than the change in the parameter input. The largest sensitivity value for the matrix model was 1.40 for stage 1 survivorship.

### Comparison of Management Scenarios

Starting with patch occupancy data for 1995, both models projected a relatively constant steady state for both clusters for the next 50 years (Fig. 4). But simulations that incorporated the effects of fire suppression by annually decreasing habitat area (incidence function model) or carrying capacity (stage-based matrix model) resulted in a decline in patch occupancy (Fig. 4). Simulation of patch removal accelerated this decline. For each of the three management scenarios, the two models produced similar population trajectories.

### Comparison of Artificial Landscapes

Our comparison of the two modeling approaches for 150 artificial landscapes showed relatively small disagreement (<20% difference in patch occupancy) for a majority (72%) of the configurations (Fig. 5), but strong model disagreement (>50% difference in patch occupancy) occurred in two regions accounting for 22% of the configurations. Maximum model disagreement for these two regions was centered at 2-ha patches separated by 50 m (small-near patches) and 32-ha patches separated by 750 m (large-isolated patches; Fig. 5). In the small-near region, the incidence function model predicted much higher patch occupancies than the stage-based matrix model. In the large-far region, the inci-

### Table 3. Analysis of the sensitivity of the incidence function and stage-based matrix models to changes in parameter estimates.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter(^a)</th>
<th>Sensitivity value(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incidence function model</td>
<td>( \alpha + 25% )</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>( \chi + 25% )</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>( \gamma' + 25% )</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>( \mu + 25% )</td>
<td>0.52</td>
</tr>
<tr>
<td>Stage-based matrix model</td>
<td>( p )</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>( \alpha + 25% )</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>( \text{fecundity + 25%} )</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td>( \text{stage 1 survivorship + 25%} )</td>
<td>1.40</td>
</tr>
<tr>
<td></td>
<td>( \text{stage 2-3 survivorship + 25%} )</td>
<td>0.32</td>
</tr>
</tbody>
</table>

\(^a\)The parameter \( p \) is the percentage of stage 1 migrants leaving a patch. All other parameters are as defined in the text.

\(^b\)Change in model output divided by the change in model input (25%).
Figure 4. Fifty-year projections of the estimated proportion of occupied patches (±SD) by scrub lizards for the south cluster (1) when habitat quality remains constant (circles), (2) when there is a constant annual decrease in habitat quality (triangles), and (3) when there is a constant annual decrease in habitat quality and elimination of two patches (squares). Projections were produced for both (a) the incidence function model and (b) the stage-based matrix model and were similar for north cluster patches (not shown).

 conceded function model predicted much lower patch occupancies than the matrix model.

Congruency Analysis of Artificial Landscapes
The congruency analysis for the small-near patch configuration indicated that no single parameter of the stage-based matrix model could be realistically modified to produce the high level of occupancy predicted by the incidence function model (Table 4a). Fecundity and stage 1 survivorship could be manipulated individually to produce congruence but only at twice the fecundity rate (22 hatchlings per female) or 1.2 times the survivorship rate (0.22) observed for scrub lizards in large patches (Branch et al. 1996). A combination of 9.9 for fecundity and 0.16 for stage 1 survivorship resulted in congruence with the incidence function model (Table 4b; Branch et al. 1996). A fecundity of six hatchlings per female would be almost half that observed for large patches, and stage 1 survivorship of 0.11 would be less than the survivorship rate in small patches.

Discussion
Model Comparison in a Real Landscape
The two approaches to modeling metapopulation dynamics differ substantially in their assumptions and data requirements. Incidence function models use simple presence-absence data, completely ignore demographic factors such as mortality and fecundity, and do not track local population size; the primary measure is whether a patch is occupied or not. In contrast, stage-based matrix models track the number of individuals within each patch. Local patch dynamics are modeled by means of demographic factors for each life stage, such as mortality, fecundity, and dispersal rates.

Despite these underlying differences, the two modeling approaches produced similar patch occupancy rates.
Comparison of Two Metapopulation Models Hokit et al.

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for lizards in Florida scrub. Moreover, both models predicted field measurements of patch occupancy with reasonable accuracy in south and north parts of the scrub landscape. Both models also accurately predicted which patches were occupied. But model agreement may have been enhanced by the prevalence of small patches, which were mostly unoccupied, and large patches (>12 ha), which were nearly always occupied (Fig. 3). This occupancy pattern is typical of mainland-island systems, which consist of large patches that act as extinction-immune mainlands and small patches that act as extinction-prone islands (Boorman & Levitt 1973; Harrison 1991; Stith et al. 1996). The dynamics of mainland-island systems are relatively simple. Also, because we parameterized our models using data from Avon Park, the accuracy and agreement of the two models may be reduced for other landscapes with more complex dynamics.

Model Comparison in Artificial Landscapes

The wide range of patch sizes and interpatch distances we modeled on artificial landscapes produced population dynamics characteristic of different types of metapopulations (sensu Harrison 1991). Some patch configurations that exhibited partial occupancy at quasi-equilibrium (Fig. 5) represent “classical” metapopulations consisting of small patches that go extinct and are recolonized. We also observed “nonequilibrium” metapopulations, in which rapid extinction of patches led to extinction of the entire metapopulation (Harrison 1991; Stith et al. 1996), and landscapes with patches that never went extinct. These differing population dynamics provided substantial opportunity to produce differences between the incidence function model and the stage-based matrix model. The models showed relatively high agreement for most landscape configurations but produced very different results in two regions, small-near patches and large-far patches.

In the small-near patch configuration, the stage-based matrix model predicted low metapopulation persistence, whereas the incidence function model predicted high persistence. Our congruency analysis indicated that the incidence function model would predict low persis-

Figure 5. Results of transient dynamic simulations for artificial landscapes with 20 patches for (a) the stage-based matrix model and (b) the incidence function model. The upper limits of the contour shading in (a) and (b) represent 20%, 40%, 60%, and 80% occupancy, respectively. Part (c) shows the difference between the matrix model and the incidence function model. For (c), the darkest shading represents differences of >50%, the lightest shading represents differences between 20% and 50%, and moderate shading represents differences of <20%.
In this landscape the stage-based matrix model predicts 0% patch occupancy, and the incidence function model predicts 99% occupancy (Fig. 5).

<table>
<thead>
<tr>
<th>Model</th>
<th>Patch size (ha)</th>
<th>Interpatch distance (m)</th>
<th>Parametera</th>
<th>Range of manipulation</th>
<th>Congruenceb</th>
<th>Valuec</th>
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<tbody>
<tr>
<td>Stage-based matrix</td>
<td>2</td>
<td>50</td>
<td>p</td>
<td>0.1–1.0</td>
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<td></td>
<td></td>
<td></td>
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<td>9.9 × 0.16</td>
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<tr>
<td>Incidence function</td>
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<td>μ</td>
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<td></td>
<td></td>
<td></td>
<td>x</td>
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<td></td>
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<td>0.03 × 22</td>
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<tr>
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<td>p</td>
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<td></td>
<td></td>
<td></td>
<td>α</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
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<td></td>
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<td>μ × x</td>
<td>0.001–0.076 × 0.974–3.0</td>
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<td>0.02 × 2.0</td>
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</table>

aAll parameter values are as in the transient dynamics simulations except for the parameter(s) being manipulated. Parameter refers to the parameter(s) being manipulated. The parameter p is the percentage of stage 1 migrants leaving a patch.
bIndicates whether the respective model’s output came within 5% of the alternative model’s output for the percentage of occupied patches.
cValue of the parameter(s) for which congruence was achieved.

In this landscape the stage-based matrix model predicts 0% patch occupancy, and the incidence function model predicts 99% occupancy (Fig. 5).

Advantages and Disadvantages of the Two Modeling Approaches

A major advantage of incidence function models over stage-based matrix models is the relatively simple field data requirements, which can be met from a single comprehensive patch survey of presence-absence. There are, however, some important restrictions on the type of system for which an incidence function model is appropriate. The study area must be completely surveyed, or the influence of unsurveyed patches may lead to overestimates of migration ability. Hanski (1999) recommends that surveyed patches constitute a small fraction of the total landscape (e.g., <20%) and that 10 or more patches should be occupied and 10 or more should be unoccu-
pied. Furthermore, there should be a sufficient number of patches (at least 30) with enough variation in patch size and isolation to provide good parameter estimates. Most important, the system should be in a state of “stochastic extinction-colonization quasi-equilibrium” (Hanski 1999). The incidence function model assumes that the landscape and pattern of patch occupancy have been fairly stable, or, if the landscape has been recently altered, that sufficient time has passed for the populations to reach an equilibrium state within the altered landscape.

In recently restored landscapes, patch occupancy may be below the equilibrium level due to a lag in colonization. But the opposite situation is much more common: landscapes that have experienced recent destruction or degradation may show higher occupancy rates than the equilibrium level due to a “crowding effect” (Lamberson et al. 1992), or temporary persistence of a few long-lived individuals. The incidence function approach also does not distinguish between sources and sinks. The presence of a species in sink patches may depend completely on immigration from a source patch (Pulliam 1988), which may recently have been destroyed. Thus, presence-absence surveys may seriously overestimate the persistence of many species that have not yet “relaxed” into an equilibrium state with much lower patch occupancies. Therefore, careful consideration should be given to the recent history of a study area.

Although stage-based matrix models have greater demands for field data than incidence function models, these models have the advantage in that they do not assume that a system is in a state of quasi-equilibrium. The occupancy of a patch is determined not simply by its size or degree of isolation, but also by the survival, fecundity, migration rates, and carrying capacities estimated for each patch. These demographic parameters can be varied from patch to patch, reflecting source-sink dynamics or differences in carrying capacity. The more mechanistic approach of explicitly modeling local population dynamics gives stage-based matrix models an advantage over incidence function models in the common situation where systems are not at equilibrium. Estimating demographic rates and other parameters used by matrix models greatly increases the demand for field data, however, and increased model complexity also brings greater risk of error propagation due to poor parameter estimation (Conroy et al. 1995; Beissinger & Westphal 1998; Hanski 1999).

Our results for the scrub landscape suggest that the incidence function approach may provide a relatively economical first step in the landscape modeling process. Within our study area, the incidence function model was much easier to parameterize than the stage-based matrix model because there was no need to estimate vital rates for lizard populations in small and large patches or to estimate local population abundance. Also, there was no need to directly estimate migration rates or to make limiting assumptions about the direction of dispersal because the patch-specific colonization probability was a function of patch isolation. With additional data (e.g., assessment of long-term stochastic effects on populations, correlation of demographic processes among patches, and dispersal rates), the stage-based demographic model presumably would be a more realistic and flexible model than the incidence function model. Nevertheless, the incidence function model performed as well as the matrix model in predicting patch occupancy and regional population dynamics in our Florida scrub landscape, and both models gave similar predictions when used to examine different management scenarios.

Our study of artificial landscapes suggests that these two models may differ substantially for some landscape configurations, highlighting an issue that merits further study. When appropriate data are available, we suggest that researchers use both techniques and examine differences in model output. Coexisting species may respond quite differently to the same spatial structure within a given landscape (e.g., Hokit et al. 1999). As conservation biologists attempt to incorporate spatial structure into the assessment of population viability, reliable landscape-level population models will be needed. The feasibility of obtaining data for population modeling varies widely among species and limits modeling approaches appropriate for each species. Understanding the limitations and applicability of different modeling approaches will become increasingly important as conservation programs undertake the challenge of managing for multiple species in a landscape context.

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Literature Cited


