Integrating Landscape and Metapopulation Modeling Approaches: Viability of the Sharp-Tailed Grouse in a Dynamic Landscape

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Abstract: *The lack of management experience at the landscape scale and the limited feasibility of experiments at this scale have increased the use of scenario modeling to analyze the effects of different management actions on focal species. However, current modeling approaches are poorly suited for the analysis of viability in dynamic landscapes. Demographic (e.g., metapopulation) models of species living in these landscapes do not incorporate the variability in spatial patterns of early successional habitats, and landscape models have not been linked to population viability models. We link a landscape model to a metapopulation model and demonstrate the use of this model by analyzing the effect of forest management options on the viability of the Sharp-tailed Grouse (*Tympanuchus phasianellus*) in the Pine Barrens region of northwestern Wisconsin (U.S.A.). This approach allows viability analysis based on landscape dynamics brought about by processes such as succession, disturbances, and silviculture. The landscape component of the model (LANDIS) predicts forest landscape dynamics in the form of a time series of raster maps. We combined these maps into a time series of patch structures, which formed the dynamic spatial structure of the metapopulation component (RAMAS). Our results showed that the viability of Sharp-tailed Grouse was sensitive to landscape dynamics and demographic variables such as fecundity and mortality. Ignoring the landscape dynamics gave overly optimistic results, and results based only on landscape dynamics (ignoring demography) lead to a different ranking of the management options than the ranking based on the more realistic model incorporating both landscape and demographic dynamics. Thus, models of species in dynamic landscapes must consider habitat and population dynamics simultaneously.*

Key Words: forest harvesting, LANDIS, landscape ecology, metapopulation dynamics, Pine Barrens, population viability analysis, RAMAS, Sharp-tailed Grouse, simulation modeling, Wisconsin

Integrando Métodos Basados en Modelos de Paisaje y Metapoblaciones: Viabilidad de *Tympanuchus phasianellus* en un Paisaje Dinámico

Resumen: *La falta de experiencia de gestión a nivel de paisaje y la limitada factibilidad de experimentos a esta escala han incrementado el uso de modelos de escenarios para analizar los efectos de diferentes acciones de gestión sobre especies locales. Sin embargo, los métodos de modelaje actuales son poco adecuados para el análisis de viabilidad en paisajes dinámicos. Modelos demográficos (por ejemplo, metapoblaciones) de especies que habitan estos paisajes no incorporan la variabilidad de los patrones espaciales de hábitats en sucesión temprana, y los modelos de paisaje no se han vinculado con modelos de viabilidad poblacional. Vinculamos un modelo de paisaje con uno metapoblacional y demostramos el uso de este modelo analizando el efecto de opciones de gestión forestal sobre la viabilidad de Tympanuchus phasianellus en la región de Pine Barrens al noreste de Wisconsin (E.U.A.). Este método permite el análisis de viabilidad con base en la dinámica del paisaje*

526

debido a procesos como sucesión, perturbación y silvicultura. El componente paisajístico del modelo (LANDIS) predice la dinámica del paisaje forestal a mediante de una serie de tiempo de mapas ráster. Combinamos estos mapas en una serie de tiempo de estructuras de parches, que formaban la estructura espacial dinámica del componente metapoblacional (RAMAS). Nuestros resultados muestran que la viabilidad de Tympanuchus phasianellus fue sensible a la dinámica del paisaje y a variables como la fecundidad y mortalidad. Ignorar la dinámica del paisaje proporcionó resultados demasiado optimistas y resultados basados solo en la dinámica del paisaje (ignorando la demografía) llevaron a una clasificación diferente de las opciones de gestión que la clasificación basada en el modelo más realista que incorpora tanto la dinámica del paisaje como la demográfica. Por tanto, los modelos de especies en paisajes dinámicos deben considerar simultáneamente tanto al hábitat como a la población.

Palabras Clave: análisis de viabilidad poblacional, dinámica de metapoblaciones, explotación forestal, ecología del paisaje, LANDIS, modelos de simulación, Pine Barrens, Wisconsin, RAMAS, *Tympanuchus phasianellus*

Introduction

The dynamics of species and the risks of extinction and decline they face are determined by their demographic characteristics, the distribution and quality of their habitat, and the changes in these factors in response to various natural processes and human-caused threats. Ecologists use two main approaches to model these dynamic processes: landscape models and metapopulation models.

Landscape models may predict changes in the structure and composition of the vegetation cover or more general changes in classes of land cover (Baker 1989). Models that focus on vegetation change vary in the ecological processes they simulate (e.g., succession, disturbance), their spatial resolution (cell size), and the extent or total landscape area they may simulate (tens to millions of hectares). Models of landscape change that emphasize vegetation change largely evolved from the early forest-simulation models of the 1970s (Botkin 1972; Ek & Monserud 1974) and the first-generation of models of spatial landscape change of the 1980s (e.g., Sklar et al. 1985). Today, a variety of approaches to the spatial simulation of vegetation change exist (Mladenoff & Baker 1999).

Metapopulation models predict the future of species existing in multiple populations–for example, in landscapes fragmented by natural or anthropogenic processes. In these models, the focus is the persistence or viability of a focal species in a given landscape, often with risk-based methods collectively known as population viability analysis (Akçakaya & Sjögren-Gulve 2000). These include occupancy models (reviewed by Sjögren-Gulve & Hanski 2000), age- or stage-structured models (reviewed by Akçakaya 2000a), and individual-based models (reviewed by DeAngelis & Gross 1992; Lacy 2000).

There have been previous efforts to link vegetation-succession or landscape models to wildlife-habitat models (e.g., Davis & DeLain 1986; Smith 1986; Hyman et al. 1991) to estimate, for example, future changes in habitats of threatened species (Pausas et al. 1997; Curnutt et al. 2000). Spatially explicit metapopulation models have in-

corporated elements of a static landscape into models that simulate the dynamics of a metapopulation that occupies the landscape (e.g., Fahrig & Merriam 1985; Lefkovitch & Fahrig 1985; Lamberson et al. 1992; Akçakaya et al. 1995). Other metapopulation models have also incorporated aspects of a dynamic landscape, for example, by modeling the capacity (or other measure of the quality) of patches to change deterministically, stochastically, or both (e.g., as a deterministic function of time since a stochastic disturbance event) (Pulliam et al. 1992; Lindenmayer & Possingham 1995a, 1995b, 1996; Akçakaya & Atwood 1997; Stelter et al. 1997; Akçakaya & Raphael 1998; Gaff et al. 2000; Johst et al. 2002; Keith 2004; Kindvall & Bergman 2004) or by considering types of patches based on occupancy and suitability and modeling the transitions between these types as stochastic events (Keymer et al. 2000; Amarasekare & Possingham 2001; Wahlberg et al. 2002).

However, none of these models included a dynamic spatial structure or a mechanistic model of landscape dynamics. Thus, by a "dynamic landscape," we mean not only a landscape in which the quality (or suitability) of the patches changes, but also one in which the spatial structure (location and number) of the patches may change. By "landscape model," we mean not only a model that predicts such changes, but also one that makes these predictions by explicitly modeling vegetation or succession dynamics based on life-history attributes of species such as shade and fire tolerance and distance and method of seed dispersal. A RAMAS GIS (defined below) is the only generic metapopulation modeling program that incorporates dynamic spatial structure, including appearing, disappearing, merging, and splitting patches (Akçakaya 2001, 2002), but it does not include an explicit landscape model that simulates vegetation dynamics. Thus, no previous model has combined landscape and metapopulation models with dynamic spatial structure to estimate extinction risks, although the need for, and possibility of, such a combination was recognized long ago (Burgman et al. 1993:215; Holt et al. 1995). Here, we integrated the
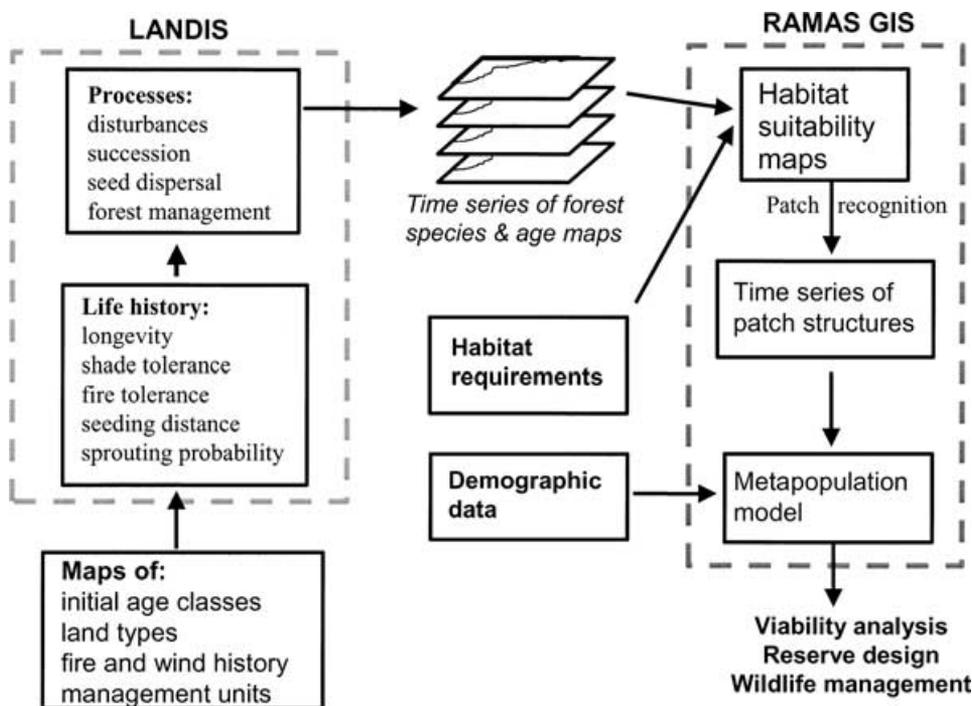
Figure 1. Integration of the landscape model LANDIS (Mladenoff et al. 1996) and the metapopulation model RAMAS (Akçakaya 2002) to model metapopulation viability in a dynamic forest landscape (source: Akçakaya et al. 2003; reprinted with permission).

landscape model LANDIS with the metapopulation model RAMAS. Both LANDIS and RAMAS are spatially dynamic, meaning that they model temporal changes in the spatial structure of the landscape and the metapopulation, respectively. Both models are generic; thus, we believe that the integrated model we used is applicable to many species that inhabit dynamic landscapes. We demonstrate the use of this integrated model by analyzing the viability of the Sharp-tailed Grouse (*Tympanuchus phasianellus*) in a dynamic landscape.

The LANDIS model (Mladenoff et al. 1996; Mladenoff & He 1999) simulates forest change by modeling tree species as 10-year age classes. It models succession based on interactions among species' life-history characteristics, site conditions, disturbance regime, and management. Life-history characteristics include longevity, age of sexual maturity, shade and fire tolerance, and seed-dispersal distance. Site conditions are encapsulated by "land types," which can be derived from climate, physiography, and soil texture and organic matter content. The LANDIS model incorporates natural processes (fire, windthrow, succession, and seed dispersal) and forest harvesting and allows many different silvicultural treatments to be modeled (He & Mladenoff 1999*a*; Mladenoff & He 1999; Gustafson et al. 2000). LANDIS has been used to model forest landscape dynamics in north temperate forests of the U.S. Lake States (He & Mladenoff 1999*b*), the Missouri Ozarks (Shifley et al. 2000), chaparral in California (Franklin et al. 2001), and Finnish boreal forest (Pennanen & Kuuluvainen 2002) and to investigate the effects of climate warming on forest ecosystems (He et al. 1999). Detailed discussion of model design and imple-

mentation are provided elsewhere (e.g., He & Mladenoff 1999*b*; Mladenoff & He 1999).

The RAMAS GIS model (Akçakaya 2002) simulates metapopulation dynamics with an age- or stage-structured model for each subpopulation. It uses landscape data to define the spatial structure of the metapopulation from the perspective of the habitat requirements of the modeled species (Akçakaya 2000*b*). Habitat dynamics are modeled by deterministic changes in model parameters, such as carrying capacity, fecundity, and survival, which are specified as time series of these parameters. Such time series are calculated from a time series of habitat maps that describe the changes in the landscape. Types of spatial change may include changing habitat quality or patch size, as well as appearing, disappearing, merging, or splitting habitat patches (Akçakaya 2001). The RAMAS GIS model has been used to analyze the effect of habitat structure on a variety of species (Root 1998; Williams et al. 1999; Kindvall 2000; Broadfoot et al. 2001; Brown et al. 2001; U.S. Fish and Wildlife Service 2001; Akçakaya et al. 2004).

Methods

In our integration of LANDIS and RAMAS, we used the landscape model to create a time series of raster maps that describe tree species composition and age distribution at each decade (Fig. 1). We then combined these maps into a time series of patch structures by using a habitat-suitability function for the Sharp-tailed Grouse. This time

Table 1. Silvicultural parameters of the timber harvest scenarios and average, final, and minimum values of the total carrying capacity (*K*) resulting from each scenario, sorted in order of decreasing average carrying capacity.

Scenario*	Minimum age of jack pine for harvest	Clear-cut size (ha)	Percent in red pine management	Average K	Final K	Minimum K
0	n/a	n/a	n/a	16400	16400	16400
4	40	259	0	14544	14607	8939
12	60	259	0	10436	8727	5141
8	40	259	50	8031	5050	5050
16	60	259	50	7475	4878	4792
5	40	4	50	5809	5386	4570
13	60	4	50	5794	5381	4565
1	40	4	0	5764	4839	4340
9	60	4	0	5743	4812	4334

*Scenario 0 assumes a static landscape with no harvest, forest growth, fire, or any other landscape change. For the other scenarios, we followed the numbering of Radeloff (2003).

series of patch structures forms the dynamic spatial structure of the metapopulation, in which the patches may be changing at 10-year time steps in the patterns summarized above. We modeled the local dynamics of the Sharp-tailed Grouse with matrix models at an annual time step, incorporating the cyclic oscillations of this species and random environmental and demographic variation.

Study Species

Sharp-tailed Grouse habitat is dominated by grasses and shrubs (Connelly et al. 1998). Although the species occupies a large range in central and northern North America, its numbers have declined greatly in many parts of its range as a result of conversion of its steppe-grassland habitat to agriculture and other forms of habitat loss (Connelly et al. 1998). In Wisconsin (U.S.A.), Sharp-tailed Grouse range has contracted since presettlement times because of loss of habitat to agricultural lands and to forests due to fire suppression (Gregg & Niemuth 2000) and forest planting. Currently, a large proportion of the species' habitat in Wisconsin is in the Pine Barrens region, with scattered habitat patches in other parts of the state. The habitat of Sharp-tailed Grouse is both fragmented (patchily distributed) and dynamic (the number, size, and distribution of patches change over time). Hence, it is well suited for demonstrating our integration of a landscape and a metapopulation model.

Study Area

The northwestern Pine Barrens region of Wisconsin is located on a 450,000-ha outwash plain with predominantly coarse, sandy soils (Murphy 1931; Radeloff et al. 1998, 1999). These soils are prone to drought and are conducive to fires. This area experienced significant fire disturbance before European settlement, when jack pine (*Pinus banksiana* Lamb.) forest and savanna dominated the landscape. Fires were common at that time and after logging and early settlement in the late 1800s through the

early 1900s. Failed farming and some reforestation have occurred, so some of the original open barrens habitat has been maintained. However, the landscape pattern has been significantly altered in the last 150 years (Radeloff et al. 1999). Local management agencies are particularly interested in the effects of forest harvest on landscape pattern in our study area because of the decline of open-habitat species (such as the Sharp-tailed Grouse) that persisted in fire-generated openings of presettlement times.

Landscape Prediction under Alternative Management Scenarios

Past forest management has created landscape patterns that differ significantly from those typical under natural disturbance regimes (Mladenoff et al. 1993; Wallin et al. 1996). It has been suggested that forest management should aim to mimic natural disturbance patterns (Hunter 1993; Wallin et al. 1994), but much is still unknown about the effects of different forest-management scenarios on landscape patterns. To help fill this knowledge gap, we simulated the change in forest landscape of the Pine Barrens under several scenarios of silvicultural management.

Using LANDIS, we simulated eight scenarios, using one of two alternative values for each of three silvicultural parameters: mean clearcut size, minimum age of jack pine for harvest, and proportion of the landscape under red pine (*P. resinosa* Ait.) management (Table 1). The minimum age limit for clearcuts in jack pine (40 or 60 years) represents the entire range of rotation lengths commonly used in jack pine management in the U.S. Lake States (Benzie 1977). The range of clearcut sizes (4–256 ha) captures the entire range of what is common in jack pine management in the U.S. Lake States. Standard deviation of the clearcut size was set to one-quarter of the mean. The nutrient-limited soils of the Pine Barrens limit the number of tree species that can be successfully grown commercially largely to jack pine and red pine. Red pine management has increased recently in the Pine Barrens to limit

future outbreaks of jack pine budworm (*Christoneura pinus pinus*) by increasing tree species diversity in the landscape (V. C. Radeloff, D. J. Mladenoff, E. J. Gustafson, R. M. Scheller, H. S. He, P. A. Zollner, & H. R. Akçakaya, unpublished data). Red pine management operates with rotation lengths about twice as long as those for jack pines, however, thereby significantly decreasing the amount of open areas present at any given time. Half the scenarios did not include management for red pine, and all stands were eligible for harvest when they approached the minimum stand age. The other half of the scenarios included red pine management on 50% of the landscape. In these scenarios, jack pine harvests would only affect red pine that was <50 years old. In areas where red pine was <50 years old, these would be harvested together with jack pine, creating a clearcut. In areas with red pine that was >50 years old, however, these older cohorts would not be harvested, and a jack pine harvest event would result in a thinning of the red pine, removing all competitors. Once red pine was 100 years old, it became eligible for red pine harvesting. The details of these landscape simulations are described by Radeloff et al. (V. C. Radeloff, D. J. Mladenoff, E. J. Gustafson, R. M. Scheller, H. S. He, P. A. Zollner, & H. R. Akçakaya, unpublished data).

Sharp-Tailed Grouse Habitat Dynamics

The results of a LANDIS simulation are a time series of raster maps describing the species composition and age structure of tree species in the landscape. We converted each of the maps into a time series of habitat maps for the Sharp-tailed Grouse by using information about the species' habitat requirements.

Habitat Requirements of the Sharp-Tailed Grouse

Habitats used by the Sharp-tailed Grouse are dominated by relatively dense herbaceous cover and shrubs, but species composition varies considerably (Connelly et al. 1998). We defined optimal habitat as areas with no trees older than 10 years and areas dominated by herbaceous vegetation, and we defined suboptimal habitat as areas dominated by 10- to 20-year old jack pine. We assigned a habitat-suitability (HS) value of 1.0 for optimal and 0.5 for suboptimal habitat.

In the input data maps for the LANDIS simulations, there are open areas in the initial landscape that are unrelated to harvesting. These are wildlife-management areas, old fields, and sedge marshes. In the LANDIS simulations these quickly convert to forest, although many of them are actually maintained as open areas. To account for this, we kept the actively maintained wildlife areas as optimal habitat (HS = 1.0) throughout the simulation, regardless of what the LANDIS simulations predicted for these areas. In essence, we assumed that the current wildlife-management areas would continue to be managed for the next 100 years.

Table 2. Sharp-tailed Grouse habitat in the Crex Meadows.

Land type	Area (km^2)[a]	Habitat (%)[b]	Habitat area (km^2)
Open water	15.99	0	0.0
Sedge marsh	38.85	50	19.4
Grass/brush	29.95	100	29.9
Pine/oak/aspen	22.50	20	4.5
Food lots	0.51	200	1.0
Total	107.79		54.9

[a]*Evrard et al. (2000).*
[b]*Contribution of each land type to optimal habitat; see text for details.*

Spatial Structure of the Metapopulation

In our study, LANDIS predicted raster maps of habitat at 100-m resolution. We converted these to habitat-suitability (HS) maps as described above and averaged them into 500-m cell size. The HS values ranged from 0 for no habitat to 1 for optimal habitat, and there was one HS map for each time step (decade) of LANDIS simulation. Based on this specification of habitat, RAMAS GIS identified the patch structure—size and location of habitat patches—for each decade. This method of patch identification is described by Akçakaya et al. (1995) and Akçakaya (2000*b*).

After the habitat patches are identified, the program calculates the carrying capacity and initial number of individuals in each patch, based on a density function. To estimate this density function, we used data of Evrard et al. (2000) on the area of different habitat types in Crex Meadows in the Wisconsin Pine Barrens (Table 2). We assumed that sedge marsh contributes half as much as optimal habitat (grass and brush prairie) to habitat quality, that pine-oak-aspen forest contributes 20%, and that food lots (where additional food is provided) contribute twice as much. Thus, we calculated a total "habitat area" (equivalent to an area of optimal habitat) by multiplying the area of sedge marsh by 0.5, the area of grass or brush by 1.0, the area of pine-oak-aspen forest by 0.2, and the area of food lots by 2.0 (Table 2). Based on these assumptions, the total "habitat area" in Crex Meadows was about 55 km^2. In this area, there was an average of 73.2 displaying males per year between 1980 and 1999 (Evrard et al. 2000; Table 2). Assuming that displaying males are over 2 years old and that they make up 9.7% of the population (based on the stable age structure of the stage matrix; see below), this corresponds to an average of 755 birds (all ages, male and female). This gives an average density of 13.7 birds/km^2 or 7.3 ha/bird in optimal habitat. This calculation is further supported by the fact that the estimated density is the same value as the average fall population observed on prime habitat on Drummond Island, Michigan, over a 7-year period (Johnsgard 1983).

With the 500-m cell size (or 25-ha cell area), the density in optimal habitat is 3.45 birds/cell. We multiplied the total habitat suitability in each patch by this number. Total habitat suitability is the sum of the habitat-suitability (HS) values of all the cells in the patch. Thus, the product of total HS in each patch and the density in optimal habitat (3.45 birds/cell) gives the maximum number of birds in that patch. We used the calculated numbers as the carrying capacities of the patches. Following Temple (1992), we assumed a ceiling-type density-dependence model.

Metapopulation Model Based on Landscape Dynamics

With the process summarized above, we obtained a time series of maps of the patch structure in the landscape. During the 100-year simulation, the number and size of patches changed, depending on the processes (such as timber harvest) modeled by LANDIS. The changes occurred because patches of suitable habitat appeared, existing patches merged because of timber harvest, or they disappeared or split into multiple patches because of forest growth. The program identified these changes and the lineage of the patches (for details of this method, see Akçakaya 2001). The result was a metapopulation model of shifting patches in a dynamic landscape. Into this dynamic spatial structure we added demographic structure, as described in the next section.

Sharp-Tailed Grouse Demographic Model

We combined the habitat-based spatial structure of the metapopulation with an age- and sex-structured stochastic model of the Sharp-tailed Grouse populations. The model included six stages; three for each sex: F0, F1, and F2+ are 0-year-old females, 1-year-old females, and 2-year-old and older females, respectively. The corresponding male stages are M0, M1, and M2+. The mating system is polygynous, with the ratio of breeding males to breeding females estimated as 1:10 (Robel 1972 cited in Temple 1992). Thus, in the model, the fecundities are multiplied by the minimum of the number of females and 10 times the number of males. Thus, we assumed that each male could mate with up to 10 females.

Survival Rates

Survival rates are similar between the sexes (Robel et al. 1972). The probability of a newly hatched female surviving to breed at 1 year of age is 0.26 (Sisson 1976 cited in Temple 1992). We assumed that all surviving females breed at age 1 and that males may potentially breed starting at age 2. Average annual adult survival in an unhunted population is estimated as 0.53 (Schroeder 1994 cited in Connelly et al. 1998). During 1983–1985, hunting mortality in Wisconsin was estimated as 30% (Gregg 1990). Since then, a permit process has been initiated and bag limits have been imposed. There are no recent studies on

Table 3. Average stage matrix used in the demographic model of Sharp-tailed Grouse.*

	F0	F1	F2+	M0	M1	M2+
F0	1.0868	2.2154	2.2154	0	0	0
F1	0.26	0	0	0	0	0
F2+	0	0.53	0.53	0	0	0
M0	1.0868	2.2154	2.2154	0	0	0
M1	0	0	0	0.26	0	0
M2+	0	0	0	0	0.53	0.53

*The model includes three stages for each sex: F0, F1, and F2+ are 0-year-old females, 1-year-old females, and 2-year-old and older females, respectively. The corresponding male stages are M0, M1, and M2+.

hunting mortality, but these measures are likely to have reduced hunting mortality. We added a hunting mortality of 25% to our model as "harvest" of all age and sex classes. We also ran simulations varying the hunting mortality from 20% to 30% to analyze the sensitivity of viability to hunting pressure.

Reproduction

Average brood size ranges from 4.1 to 9.4, and offspring per breeding female is 6.1 (Robel et al. 1972; Connelly et al. 1998). However, these figures may reflect observations made substantially after hatching and hence may reflect part of the first-year mortality. For our model, an estimate of hatchlings per female is needed because survival estimates are available from hatching to next breeding.

Average clutch size is 11.8 eggs, and the proportion of eggs that hatch ranges from 87% to 92%, with an average of about 90% (Connelly et al. 1998). There is only one brood per season, so hatchlings per female per year can be estimated as 10.6. However, clutch size is lower (9.4–11.6) in renesting attempts (when the first nest is destroyed). The proportion of breeders renesting and the proportion of nonbreeders (whose nesting attempts all fail) are unknown. Thus, as a compromise, we assumed 8.36 hatchlings per female per year, the average of the two estimates (6.1 and 10.6). We assumed a sex ratio of 1:1 at birth.

We assumed a post-breeding census: the first age class (age 0) consists of hatchlings, which breed by the next census. Thus, age-0 fecundity = $0.26 * 8.36 = 2.17$, and age 1+ fecundity = $0.53 * 8.36 = 4.43$. These fecundities are divided equally between female and male offspring (e.g., average age 1+ fecundity = 2.22 daughters per female; Table 3). We varied fecundity plus and minus 5% to analyze the sensitivity of results to the uncertainty in this parameter.

Population Cycles

Sharp-tailed Grouse populations in Wisconsin have a 10-year cycle (Evrard 2000). The generation length of the species, based on the above estimates of survival and
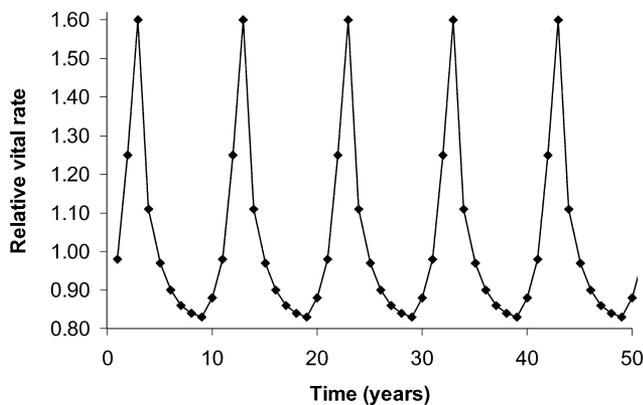
Figure 2. Time series of relative vital rates (multipliers for survival and fecundity) used to model population cycles in the Sharp-tailed Grouse model. There are 10 multipliers in each cycle of 10 years. The product of the 10 numbers is 1.00.

fecundity, is about 2.1 years. Thus, these cycles are not based on the age structure or density dependence of the species but most likely on its relationships with other species. Although the causes of these cycles are not fully known and data are not sufficient to model the trophic interactions that might cause these cycles in the Sharp-tailed Grouse, it is reasonable to assume that the proximate causes of these cyclic changes in the abundance and age structure of any particular species are changes in its fecundity and survival rates. Thus, the effect can be realistically simulated with oscillating vital rates. We added cyclicity to the fecundities and survival rates by multiplying each stage matrix elements with a "relative vital rate" coefficient that changed with a 10-year period (Fig. 2). The product of these 10 coefficients was 1.0, so they do not affect the long-term growth rate of the population.

Environmental Variability

Several other environmental factors, independent of the 10-year cycle discussed above, cause fluctuations in Sharp-tailed Grouse populations. Mortality increases during severe winters, and reproductive success may be determined by soil moisture because of its influence on cover and food (Connelly et al. 1998). Temple (1992) used coefficients of variation (CV) of 40% for fecundity, 30% for juvenile survival, and 20% for adult survival. His model did not include population cycles, however, which add a lot of temporal variability. We used 30%, 20%, and 5% for the CVs of fecundity, juvenile survival, and adult survival, respectively, and sampled these vital rates from lognormal distributions.

Dispersal

We used the dispersal-distance function $M_{ij} = a \exp(-D_{ij}/b)$, where M_{ij} is the proportion of individuals in

the source population j that move to the target population; i, a, and b are the function parameters; and D_{ij} is the distance between the two populations. To estimate the parameters, we used data from Robel et al. (1972:95; weighted average for the two locations). According to these data, the proportion of dispersers (individuals moving more than 0.8 km) is 0.582. The average distance traveled by a dispersing juvenile female is 18.96 km. Based on the juvenile female dispersal distance, we calculated b as $-\ln(0.5) * 18.96 = 13.14$ and a as $0.582/b = 0.0443$. Based on the average dispersal distance of the other stages, we calculated their relative dispersal rates as 0.33, 0.66, 0.44, and 1.0 for adult males, adult females, juvenile males, and juvenile females, respectively. We used the relative dispersal rates to calculate the proportion of each age and sex class dispersing, based on the dispersal-distance function.

Simulations

We ran nine simulations: eight simulations with timber-harvest scenarios that resulted in a dynamic landscape as described above and one simulation (scenario 0) based on the initial landscape (year 0 in LANDIS simulations). Thus, under scenario 0, the habitat structure and distribution observed for year 0 did not change for the duration of the simulation. We ran each RAMAS simulation for 1000 replications. The duration of the simulations was set at 100 years. The results of the simulations were summarized in terms of risk of decline to a set of thresholds (500, 1000, and 1500 birds) within 100 years.

Results

The Sharp-tailed Grouse habitat was distributed throughout the Pine Barrens region, with larger patches of suitable habitat in the middle and south sections of the region (Fig. 3). Analysis of the initial landscape (year 0 in LANDIS simulations) with respect to the habitat requirements of the Sharp-tailed Grouse resulted in a total carrying capacity of 16,400 birds, distributed among 18 habitat patches.

Different timber-harvest scenarios caused different patterns of change in the landscape, including the amount of available habitat, measured in terms of the total carrying capacity (K) of all habitat patches (Table 1; Fig. 4). Scenario 0 (which assumed no habitat change) resulted in the largest K. The four scenarios (4, 8, 12, and 16) with a large clearcut size resulted in a larger average and final K than the four scenarios with a small clearcut size (Table 1).

The risk of decline of the Sharp-tailed Grouse to 500, 1000, and 1500 birds within the next 100 years was different under different scenarios (Table 4). Risks were highest with scenarios 8 and 16 and lowest with scenarios 0 and 4. Other measures of viability—expected minimum
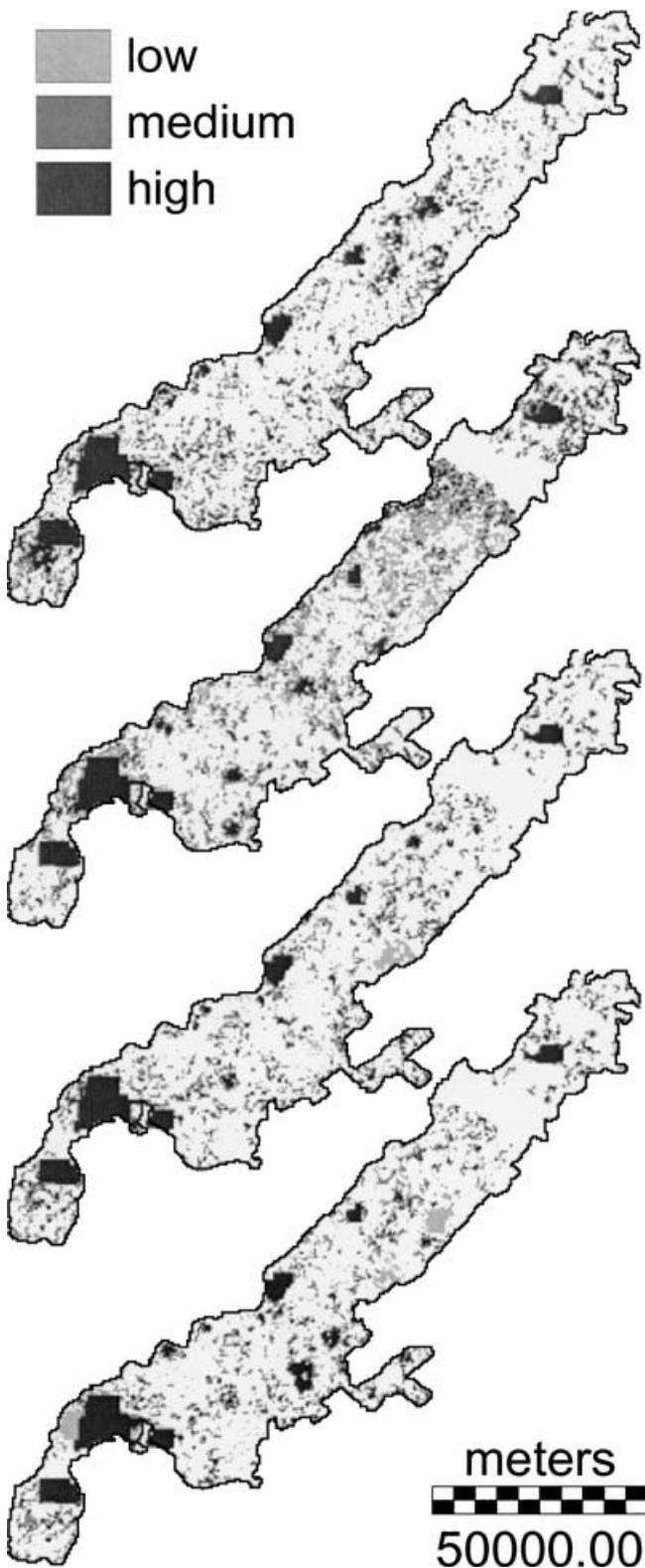
Figure 3. Distribution of Sharp-tailed Grouse habitat in the Wisconsin Pine Barrens region at year 0, 20, 40, and 80 (from top to bottom), under scenario 4 (Table 1).

abundance (McCarthy & Thompson 2001) and total abundance at the end of the simulation—gave similar results (Table 4). When landscape dynamics were ignored (scenario 0), the risk of decline to 1000 birds within 100 years was <0.0005. For scenarios with landscape dynamics, this risk ranged from 0.005 to 0.916 (Table 4).

The results of all scenarios simulating landscape dynamics (i.e., all except for scenario 0) were sensitive to changes in the value of average fecundity (Fig. 5). Risk of decline to 1000 birds within 100 years ranged from 0.05 to 1.0 when fecundity was 5% lower than the medium fecundity, and it ranged from 0.0 to 0.49 when fecundity was 5% higher than the medium fecundity. The results were also sensitive to hunting mortality. Changing hunting mortality from 20% to 30% increased the risk of decline to 1000 birds from 0–0.05 to 0.57–1.0 for scenarios with landscape dynamics (Fig. 6).

Discussion

One of the important issues in linking two spatially explicit models is the correspondence between spatial and temporal scales of the two models. In our integration of RAMAS and LANDIS, we kept both the temporal and the spatial scales flexible in order to use the most appropriate scale for each model. The rate of landscape change was far slower than that of grouse population dynamics; hence, the time step of the landscape model was longer (decadal) than that of the metapopulation model (annual). The 100-m spatial resolution of the landscape model is realistic for simulating vegetation dynamics at the stand level, but it is unnecessarily high for simulating grouse dynamics at the population level. Even at the individual level, the 500-m spatial resolution (25-ha cell size) we used would be appropriate, considering that the home range of this species in Wisconsin is up to 259 ha (Connelly et al. 1988). Our model is a patch- or population-based model, however, and each patch consisted of dozens to hundreds of cells, providing sufficiently fine detail.

Our results indicate that the viability of the Sharp-tailed Grouse metapopulation in the Pine Barrens region depends on both landscape dynamics and demographic variables such as fecundity and mortality. The timber-harvest scenario affected the amount of suitable habitat for the species, how the habitat changed over time, and the viability of the species. However, these effects were not always correlated. For example, although scenario 12 was one of the scenarios with the largest amount of habitat (total carrying capacity), it was also one of the three worst scenarios in terms of viability (Tables 1 & 4). Similarly, scenario 9 resulted in the smallest amount of habitat (lowest average and final *K*) but was one of the better scenarios in terms of viability. Such results suggest that ranking management options only in terms of the habitat they provide
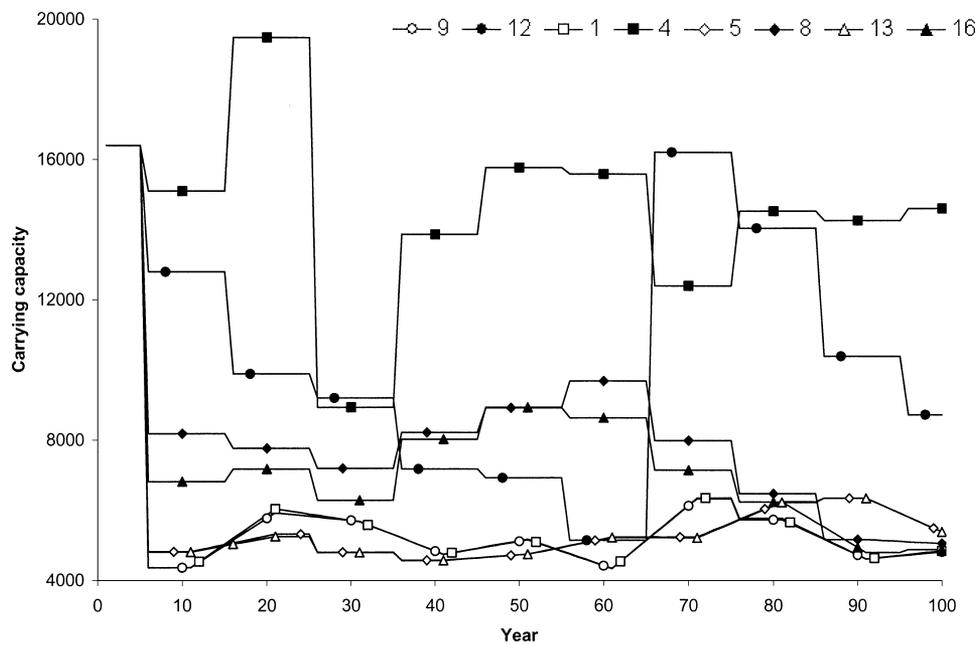
Figure 4. Change in the total carrying capacity of all habitat patches (in terms of the number of grouse) with eight timber harvest scenarios. Harvest scenarios depicted in key are described in Table 1.

for threatened or declining species while ignoring the demography of the species may be misleading.

On the other hand, our results also suggest that ignoring changes in the landscape may also be misleading. The simulations that assumed no change in habitat (scenario 0) resulted in the highest viability. In other words, ignoring landscape dynamics overestimated viability and gave results that were too optimistic compared with the more realistic simulations that incorporated landscape dynamics.

The reason for these results may be complex interactions between habitat change (appearance, disappearance, splitting, and merging of habitat patches over time) and population change (growth and dispersal potential). Johst et al. (2002) demonstrated that long-term metapopulation persistence depends on rates of patch destruction and regeneration and on rates of population growth and colonization. They argued that these four variables may have different time scales, violating the assumption of time-scale separation in occupancy-type metapopulation models. This is further complicated in cases where the spatial structure of the patches may also be dynamic because of merging and splitting patches.

Methods that do not incorporate dynamics in both habitat and demography may give an incomplete assessment of the management options. This is likely to be especially important in species, such as the Sharp-tailed Grouse, that live in fragmented landscapes and are dependent on temporary habitat patches. The viability of such species depends on the balance between the rate of appearance and spatial arrangement of patches on the one hand and the reproductive capacity of the species on the other. Consequently, the viability of the species depends sensitively both on the spatiotemporal pattern of landscape changes

Table 4. Viability of Sharp-tailed Grouse in the Pine Barrens under nine scenarios of landscape change, in terms of risk of decline, expected minimum abundance, and percentiles of abundance in year 100.[*]

	Probability of decline to threshold T *within 100 years*			Expected minimum total abundance	Percentiles of distribution of the total number of individuals in year 100				
Scenario	*T = 500*	*T = 1000*	*T = 1500*		*5th*	*25th*	*50th*	*75th*	*95th*
0	0.000	0.000	0.000	5385	5409	6938	8200	9337	10793
4	0.000	0.005	0.064	2408	2033	3162	4178	5295	6919
13	0.000	0.017	0.573	1454	1787	2190	2500	2874	3314
5	0.000	0.020	0.559	1453	1789	2198	2522	2889	3399
9	0.000	0.082	0.818	1299	1221	1623	1929	2319	2774
1	0.000	0.099	0.833	1282	1143	1558	1896	2234	2754
12	0.013	0.256	0.768	1240	1412	1787	2056	2338	2924
8	0.150	0.906	1.000	720	388	618	779	990	1272
16	0.226	0.916	1.000	670	660	1136	1525	1889	2477

[*]*Scenarios are sorted in order of increasing risk of decline.*
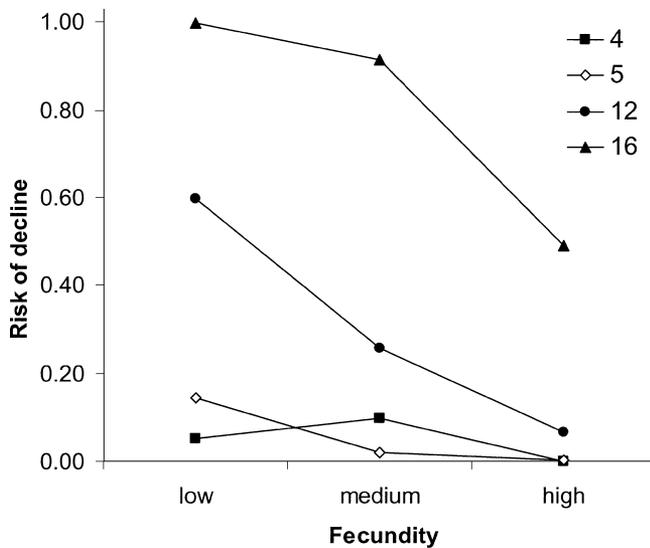
Figure 5. Effect of Sharp-tailed Grouse fecundity on the species' risk of decline to 1000 birds within 100 years under different scenarios of forest harvest (4, 5, 12, 16). Low and high fecundity values are 5% lower and higher than those described in the text, respectively. Harvest scenarios are described in Table 1.

Figure 6. Effect of hunting mortality on the risk of decline to 1000 birds within 100 years for forest harvest scenarios 4, 5, 12, and 16 (see Table 1). The results with the scenarios not shown here fell between the results for scenarios 4 and 16.

resulting from different silvicultural practices (Table 4) and on demographic variables such as fecundity (Fig. 5) and mortality (Fig. 6). Thus, neither habitat dynamics nor demographic properties alone can predict whether a certain forest-management plan will result in a viable population of Sharp-tailed Grouse. The only way such an assessment can be made is by considering both habitat dynamics and population dynamics simultaneously.

Our model represents the first attempt at establishing a spatially explicit link between the landscape and metapopulation approaches, allowing an analysis of population viability based on landscape dynamics brought about by natural and human-mediated processes such as succession, disturbance, and silviculture. In addition, the integration of two generic, spatially explicit models allows application of this approach to other cases of species living in fragmented and dynamic habitats. The most important challenge to the practical use of this approach in the conservation and management of species in dynamic landscapes comes from obtaining sufficiently precise estimates of model parameters. Future developments focusing on statistical methods of data analysis and parameter estimation would greatly enhance the usefulness of this approach.

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