CHAPTER

Methods for Determining Viability of Wildlife Populations in Large Landscapes

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The viability of a species in a given geographic region is often expressed with measures such as risk of extinction or decline, expected time to extinction, or chance of recovery. Population viability analysis (PVA) uses a variety of models to predict such measures of viability based on demographic data (such as censuses, mark-recapture studies, surveys and observations of reproduction and dispersal events, presence-absence data) and habitat data. Whether a species can persist in a particular landscape, and at the population size the landscape can support, is dependent on the demography of the species and on the spatial distribution, quality, amount, and temporal dynamics of its habitat.

Habitat by itself does not determine whether a species will persist, decline, or recover. There are many situations in which a species may not be viable despite plentiful habitat. One common cause of this disconnection is the effect of threats unrelated to habitat, such as harvest by humans, diseases, and exotic species that are competitors, predators, or parasites. Another common reason is the interaction between the spatial distribution of the habitat and the ecology of the species. Even if there is sufficient habitat, if it is fragmented into patches too small to support populations or too isolated to allow recolonization, the species will not be viable.

Similarly, demography by itself cannot determine how much habitat is required to ensure the viability of the species and where it should be located. Equivalent demographic characteristics (such as survival rates and fecundities) may result in a viable population in one landscape but a declining or extinction-prone population in the other. Depending on the quality and the level of fragmentation of the habitat, population sizes in the latter landscape may be too small for the species to escape the perils of demographic stochasticity, genetic problems, and Allee effects. At small population sizes, these chance effects tend to be the predominant determinant of a species' persistence (Gilpin and Soulé 1986). Even the same demography and the same area of habitat can result in different population dynamics and different chances of persistence, depending on the spatial configuration and heterogeneity of the habitat and intervening matrix, as well as temporal changes in the habitat (including frequency and size distribution of disturbances). Therefore, practical conservation planning in large landscapes must take demography, ecology, and habitat into account, and rely on measures that can integrate the effects of these different factors. Viability is one such measure, and PVA models provide the integrative tool.

Population viability analyses focus on specific types of questions that are relevant to the conservation of wildlife species in large landscapes (Beissinger et al., this volume). Such questions include the probability of persistence of a species in a particular landscape; the cumulative or individual effects of past or future impacts on the species' risk of extinction or decline; and the potential for alternative management and conservation actions to increase the species' chances of survival and/or recovery in the landscape.

Because of its ability to link habitat and demography, PVA can use simultaneously different types of information (see next section) and can consider cumulative and synergistic effects of different types of impacts. Although certain threat factors primarily affect a species' habitat (such as urban sprawl or logging) and others affect its demography (such as harvest or introduced predators), many factors have effects on both habitat and demography (such as pollution, climate change, roads, suppression or increase of fire, invasive species).

The ability to link habitat and demography also allows the user of PVA to compare different types of conservation actions. For example, if a given area of habitat does not support a viable population, potential conservation measures include those that are explicitly habitat-related, such as improving habitat quality, designating a larger area as critical habitat, and changing the spatial configuration of the habitat, as well as a number of measures not directly related to the area and configuration of habitat. These include re-introductions, translocations, regulation of harvest in adjoining areas (which may otherwise act as sink populations because of high exploitation rates), removal or suppression of exotic species, increasing connectivity, and precautions against catastrophic events such as disease epidemics. Methods such as PVA that integrate demographic and habitat information can assess the combined effects of all such conservation measures in terms of the increased viability of the species.

RELATIONSHIP OF PVA TO OTHER METHODS

There are several other quantitative methods and models used for planning wildlife conservation in large landscapes. Population viability analysis is not an alternative to these other methods, but a complementary approach that often uses their output to answer a range of the specific questions discussed previously that other methods cannot address as efficiently (Brook et al. 2000). Indeed, the information these methods provide helps to determine both the complexity of the PVA that can be developed and the types of questions it can be used to address. The relevance of these methods to PVA is briefly discussed in the following paragraph.

Geographic information system (GIS) methods underlie the development and analysis of many of the spatially explicit PVA models. Habitat models predict the distribution of suitable habitat (Dijak and Rittenhouse, this volume; Larson et al., this volume; Niemuth et al., this volume; Fitzgerald et al., this volume), which can determine the spatial structure of the PVA models, as well as characteristics of their spatial units (e.g., carrying capacity of populations or quality of territories). Statistical analyses of population trends allow calibration of demographic models or, if independent of demographic data, used in model construction for the validation of demographic models. Landscape-level measures such as connectivity and fragmentation provide information for the spatial structure and dispersal rates for PVA models. Landscape models (such as LANDIS [He, this volume] and LMS [Oliver et al., this volume]) predict the temporal changes in the landscape, which are then integrated into PVA predictions through simulation of dynamic metapopulation structures (Bekessy et al., this volume; see examples later). Reserve selection methods (Flather et al., this volume) find configuration of protected areas that maximize species representation, and are moving toward considering species viability as well.

ISSUES FOR LARGE-SCALE PVA APPLICATIONS

For wildlife populations in large landscapes, viability analysis requires careful consideration of the issues of spatial scaling and heterogeneity, habitat structure and connectedness, and temporal dynamics of the landscape.

Spatial Extent

The determination of the spatial extent (i.e., geographical range size and boundaries) of the modeled populations is an important issue. For example, when PVA is used to assess the potential impact of a threat to the viability of a wildlife population, and the threat affects only a small part of the landscape, then there might be several alternative ways of selecting the “assessment population,” which is the population for which the increased risk due to the specific threat is estimated. Further, the relative importance of such threats to conservation management of the species as a whole can be understood only if its scope is properly contextualized (e.g., the risk of a fire that causes 90% mortality but affects only 10% of a species’ range may not be worth managing, whereas a disease that kills 20% of individuals but has a range-wide impact may be). As such, the assessment population may be different from the biological population or metapopulation, and its spatial extent is often more a social (thus, regulatory) issue than a scientific issue. If the assessment population is limited to the affected area, the results will be more sensitive to the potential impacts but less relevant for the overall viability of the population. In such cases, it may be better to assess impacts at multiple spatial extents. Thus, different scales and extents may be needed for different purposes.

Spatial Resolution

In our context, resolution refers to the size of the smallest spatial unit of a model. For PVA, the relevant measure of resolution is related to the spatial unit of the demographic entity being modeled. The demographic entity can be an individual or a population. Thus, for individual-based models, the resolution can be a territory or home range; for population-based models, it can be the smallest habitat patch that supports a subpopulation. For grid-based landscape models, it may be some arbitrarily designated unit that can be defined conveniently within a GIS based on remote sensing.

Most spatially explicit and individual-based PVA models for large landscapes represent the landscape as discrete home ranges or territories of the modeled species. Each territory is often assumed to support one breeding pair. This is often a reasonable assumption, but in many cases the territories do not all have similar sizes or shapes, are often not distributed uniformly in the landscape, and their distribution, sizes, and shapes can change frequently depending on the population size, composition, the level of resources, and the degree of competition. In such cases, models based on a spatially uniform or temporally fixed pattern of territories may miss important structural or dynamic characteristics of the landscape that affect viability.

Most spatially explicit and population-based PVA models for large landscapes represent the landscape as discrete habitable patches within a surrounding matrix that may allow dispersal but does not support populations. Each discrete habitable patch is assumed to support one population (sometimes called a subpopulation of a metapopulation). This is often a necessary simplification in situations in which it is possible to identify habitat patches on the basis of geophysical and ecological landscape metrics, but where detailed point-based presence-absence data are unavailable. When such data are available, they can be used to generate a habitat map using niche modeling (also called species distribution modeling), and the habitat map in turn can be used to identify populations. A biological population can be defined as a group of regularly interbreeding (i.e., panmictic) individuals. One approach to delineating a population is to rephrase the question as: How far apart must two individuals be in order to be considered in different populations? The answer depends on the characteristics of the landscape, as well as a spatial measure (e.g., “Neighborhood distance” in Akçakaya 2005) related to the possibility of interbreeding (for example, the frequency distribution of movement distances of the species or the size of its home range). This approach, combined with modeling and prediction of suitable habitat, is used in habitat-based metapopulation models to delineate populations (Akçakaya 2000, 2005).

There are two other related measures of resolution. One is the size of the smallest unit for applying conservation or management actions. The other is the cell size of the landscape maps (e.g., vegetation maps and satellite imagery) that often form the basis for inferring the distribution of habitat in a PVA model. Although these separate measures of resolution are often different from each other and from the model resolution as discussed previously, sometimes by orders of magnitude, they nevertheless should be consistent with the resolution of the PVA model itself, as defined earlier. For example, if the home range of a species is in the order of 1 ha, habitat maps used as a basis for an individual-based and a population-based model should have cell sizes of much smaller than 1 ha, and smaller than but close to 1 ha, respectively.

Connectivity

Connectivity is the degree to which organisms can move through the landscape. Common measures of connectivity include dispersal rate (proportion of individuals moving from one habitat patch to another) and dispersal probability (probability of an individual moving from one patch or cell to another). Defining connectivity in the context of PVA requires first establishing the model's spatial resolution (the spatial unit of the demographic entity being modeled; see previous discussion). Incorporation of connectivity into PVA models depends on model type. In many models, dispersal rates or probabilities are distance-dependent, age- and/or sex-specific.

Connectivity of wildlife populations in large landscapes is often vital to their persistence in the landscape. However, defining connectivity as a conservation and management goal by itself may be counterproductive. Although increased dispersal often increases viability, this is not universal (see Stacey et al. 1997, Beier and Noss 1998, Lecomte et al. 2004). Even when it does, increasing dispersal by building or maintaining habitat corridors may not be the best option. Whether or not such conservation actions are useful depends on many factors, including the behavior of the species in corridors, relationship between dispersal and viability, and cost of, and alternatives to, corridors (Akçakaya et al. 2007).

Spatial Heterogeneity

The larger the landscape, the more heterogeneous it is likely to be. For PVA models, spatial heterogeneity refers to the variability in habitat quality and other environmental factors across the landscape. This spatial variability is expressed in PVA models as differences in population parameters or occupancy rates in different parts of the landscape—for example, in different populations. The parameters most commonly used to express this variability include population size or density, carrying capacity and vital rates (survival and fecundity), and foraging probability and home range size in individual-based models.

Other aspects of demography also are likely to change across space. For example, catastrophe probabilities and associated effects, dispersal rates, variability in vital rates and other parameters, temporal trends in carrying capacity and other parameters, and type and strength of density dependence (including Allee effects) are among the parameters that may vary among populations as a result of differences in the habitats and other environmental factors they experience.

There are two important aspects of spatial variability that result from its interaction with temporal variability. One is the temporal change in spatial patterns of habitat quality, discussed in the next section. The other is the spatial correlation in temporal variability, which is often expressed as correlation of vital rates or other stochastically varying parameters among the different populations in the landscape. Spatially correlated fluctuations in population parameters are brought about by environmental factors that are often correlated even at relatively large distances (e.g., large-scale climatic factors such as rainfall, temperature, flow rate), and in turn result in more synchronized declines and extinctions among populations (Akçakaya and Ginzburg 1991, Burgman et al. 1993, LaHaye et al. 1994). In a large landscape, models based on an assumption of completely correlated fluctuations among populations are likely to be invalid, at least for those populations that are far away from each other. On the other extreme, models based on an assumption of uncorrelated fluctuations among populations are likely to be invalid for those that are close by, and underestimate the temporal variability of population size and therefore the extinction risk of the metapopulation. Estimating correlations correctly is particularly important in large landscapes because neither of the two simplifying assumptions commonly made in models is likely to be valid.

Temporal Dynamics of the Landscape

An important factor governing the viability of species in large landscapes is the effect of landscape dynamics on the temporal variability of the habitat and hence on the dynamics of the wildlife populations. Landscapes change according to seasons, climatic fluctuations (e.g., droughts, El Ninô events), disturbances (e.g., fire and windthrow) and succession, as well as human impacts (e.g., urban sprawl, global climate change, and agricultural expansion). For a wildlife species in such a dynamic landscape, these changes are manifested as monotonic trends or oscillatory changes in both population characteristics (e.g., carrying capacity and average fecundity) and in metapopulation attributes (e.g., number and sizes of populations and distances among them).

Viability of species in these dynamic landscapes depends on the interaction between landscape change and the species' ecology (i.e., its ability to disperse between and function within the habitat patches). Some PVA models incorporate aspects of a dynamic landscape in a static spatial structure—for example, using a metapopulation model with fixed number of populations whose carrying capacity changes over time (Pulliam et al. 1992, Lindenmayer and Possingham 1996, Stelter et al. 1997, Akçakaya and Raphael 1998, Johst et al. 2002, Keith 2004). Such changes can be deterministic (for example, to simulate forest growth) or stochastic (to simulate the effects of random disturbances such as fires) or both (e.g., using a deterministic function of time since a stochastic disturbance event).

Other PVA models also incorporate a dynamic spatial structure that arises from habitat patches splitting, merging, appearing, and disappearing as the species' habitat changes (Akçakaya 2001, Akçakaya and Root 2003). This approach has been applied to landscape changes brought about by timber harvest, succession, and natural disturbances (Akçakaya et al. 2004, 2005; Wintle et. al 2005; Bekessy et al., this volume).

One temporal process in particular—climate change—has encouraged the development of modeling approaches to determine temporal range shifts (e.g., Keith et al. 2008). There are now many documented examples of a species' bioclimatic tolerance limits shifting toward higher latitudes and upward in elevation as the planet warms (Araujo and Guisan 2006, LaSorte and Thompson 2007). There are also instances of the spread of woody vegetated habitats of threatened species caused by the enrichment of atmospheric CO_2 or altered fire regimes (Bond et al. 2005, Bowman et al. 2006). Given the global extent of climate change, it is likely that the incorporation of such spatio-temporal changes will become routine in future PVA modeling.

TYPES OF MODELS AND EXAMPLES OF THEIR APPLICATIONS

What model should be used to determine viability of species in large landscapes? The answer very much depends on the type of data that are available for model parameterization, the ecology of the species under consideration, the nature of the conservation management question being asked, and the available expertise (Dunning et al. 1995, White 2000). In this section, we describe four commonly used approaches and provide a selection of examples to illustrate their application. A brief summary of the model types and further examples are given in Table 17-1. At the end of this section, we also briefly consider issues of model selection and multimodel inference.

Occupancy Models

We often know very little about the ecology and demography of threatened species. By virtue of their rarity, they are difficult and expensive to study, especially across large landscapes, and long-term monitoring data are usually not available. That said, one form of information that is often routinely collected, or can be

Table 17-1 Types of Population Viability Models and Examples of Their Use

Model Type	Best For	Examples
Occupancy models	Equilibrium metapopulations High rate of local extinction and recolonization Limited demographic data Small, short-lived organisms (e.g., invertebrates) Large number of patches	Granville Fritillary (Hanski et al. 1996) Arboreal forest marsupials (Lindenmayer et al. 1999)
Lattice (grid-based) models	Relatively uniform or undisturbed landscapes Landscapes with continuous environmental gradients Locally abundant organisms	*Aster kantoensis* (Shimada and Ishihama 2000) Asian Water Buffalo (Brook and Bradshaw 2006*a*) Vegetation patterns (Molofsky and Bever 2004)
Demographically structured metapopulation models	Declining populations Locally abundant organisms Vertebrates and plants Large or dynamic landscapes Sufficient demographic data	Sargent's Cherry Palm (Maschinski and Duquesnel 2006) Woodland Brown Butterfly (Kindvall and Bergman 2004) Chinook Salmon (Ruckelshaus et al. 2004) Tree Frog (Pellet et al. 2006) Eastern Indigo Snake (Breininger et al. 2004) Bell's Sage Sparrow (Akçakaya et al. 2005) Brown Creeper (Wintle et al. 2005) Magpie Geese (Brook and Whitehead 2005) Carpentarian Rock Rat (Bowman et al. 2006) Ocelot (Haines et al. 2006)
Individual-based models	Very small populations Abundant demographic and behavioral data Large-bodied, territorial species Modeling impact of genetic threats Determining emergent behaviors	*Micoures demerarae* (Brito and Fernandez 2000) Northern Spotted Owl (Lamberson et al. 1996) Leadbeater's Possum (Lindenmayer and Lacy 1995) *Panthera gombaszoegensis* (O'Regan et al. 2002) Community assembly (Hraber and Milne 1997)

acquired at an acceptable cost, is presence-absence data used to assess site occupancy and distributional ranges. If discrete habitat patches can also be defined, then simple occupancy models can be used to provide a crude assessment of population viability. Occupancy models, which consider whether a species is either present or absent from a patch, were first described within the theoretical context of simple metapopulations (Levins 1970). Although early work considered only the turnover of patch tenancy within a patch network, while ignoring the distance between patches and the size of the populations that these patches could support, more recent advances have relaxed these restrictive assumptions.

Certainly, the most widely adopted occupancy model to be used for practical conservation problems is Hanski's (1994) incidence function model (IFM). This model can be fitted to presence-absence data, while taking explicit account of the location and size of patches to estimate turnover (a dynamic equilibrium between extinction and recolonization is an underlying assumption), and hence long-term viability. The best-known and exemplar application of the IFM is to the Glanville fritillary butterfly (*Melitaea cinxia*), found scattered throughout the grassy meadows of southwest Finland. Extensive metapopulation survey data on this species, covering hundreds of subpopulations over more than a decade, have allowed extensive refinement and testing of the model and associated theory in spatial ecology (Ovaskainen and Hanski 2003).

There are some clear advantages to using the IFM and related stochastic patch occupancy models, including (1) they are relatively easy to parameterize given quite minimal "snapshot" data taken at a landscape-scale; (2) more sophisticated state transition models can be used to incorporate additional information about measured levels of patch turnover, if available (Sjögren-Gulve and Ray 1996), and GIS data on landscape structure and habitat quality can also be integrated into the basic IFM, if available (Moilanen and Hanski 1998); (3) conversely, Bayesian approaches have been developed to augment model fitting and take account of uncertainty better when required information on the study metapopulation is unavailable (O'Hara et al. 2002); and (4) user-friendly generic software tools such as META-X (Grimm et al. 2004) and SPOMSIM (Moilanen 2004) are available to perform the necessary calculations; these also allow the user to implement optimization algorithms (e.g., for reserve design) and undertake scenario modeling (e.g., patch deletion to simulate habitat loss).

Equally, there are obvious limits to inference that can be made with occupancy models (Baguette 2004). For instance, they ignore local population dynamics and assume a disconnect between the time scale of dispersal events and the rate of population growth or decline within patches considered effectively instantaneous, and therefore not amenable to management. Both assumptions may be unrealistic for large, long-lived species with large distributional ranges. Empirical tests of IFM predictions using real-world data have given mixed results, working quite well for some mammal species but poorly for others (Lindenmayer et al. 1999). Even in the case of the well-studied Glanville fritillary, uncertainties in parameter estimation precluded a precise estimation of extinction risks, although the rank order of management scenarios was robustly predicted (Drechsler et al. 2003).

Another limitation of IFM is the equilibrium assumption. Many species of conservation concern are declining for various reasons, which invalidates this assumption. In more detailed models (discussed later), such declines are modeled in various ways—for example, by a gradually declining carrying capacity or by a density-independent decline due to low survival or fecundity. In addition, habitat loss is often accompanied by habitat fragmentation in which the number of patches increases as they split and become smaller. Such changes are incorporated in the more detailed models, but not in IFM, which limits their applicability to threatened species (Pellet et al. 2006).

Lattice (Grid-Based) Models

As described previously, most spatially explicit population dynamics models divide the landscape into a number of discrete units, such as patches. Each patch is then considered to either support a resident subpopulation, or to be vacant. Alternatively, each patch can be modeled as a distinct and structured demographic unit, which may or may not be linked to other patches by dispersal (see next section). Lattice models, however, are not concerned with patches (Nakamaru 2006). Landscapes are instead treated as continuous, gridded surfaces, and the species of interest has a defined probability of moving between adjacent cells within a fixed time step. In lattice models, the entire landscape is considered to be usable, with the relative quality of each cell defined by a Habitat Suitability Index function based on environmental variables. This method considers explicitly the spatial and temporal variation of environments and the influence that this heterogeneity exerts on organisms using these landscapes. Moreover, the raster-based format used by GIS provides a convenient way to integrate the different forms of information required for parameterizing lattice models (e.g., geophysical landscape attributes and vegetation pattern inferred from satellite imagery; With 1997).

Population dynamics can be simulated within each grid cell, although usually in a simplified (nonstructured) form, such as via a density-dependent scalar growth function. For instance, a lattice model of feral ungulates in Kakadu National Park, northern Australia, used a theta-logistic function to model densities within 10 km × 10 km grid cells (Brook and Bradshaw 2006*a*). The model was habitat driven in that animal densities were ultimately linked to the habitat quality of each cell (e.g., vegetation type, distance to water), which determined carrying capacity. The proportion of animals that dispersed to adjacent cells depended on the density within the originating cell. This model, when linked to a previously determined functional response curve developed for buffalo (*Bubalus bubalis*) and pigs (*Sus scrofa*), was used to determine the optimal spatial configuration of helicopter-based culling. By targeting individual grid cells or

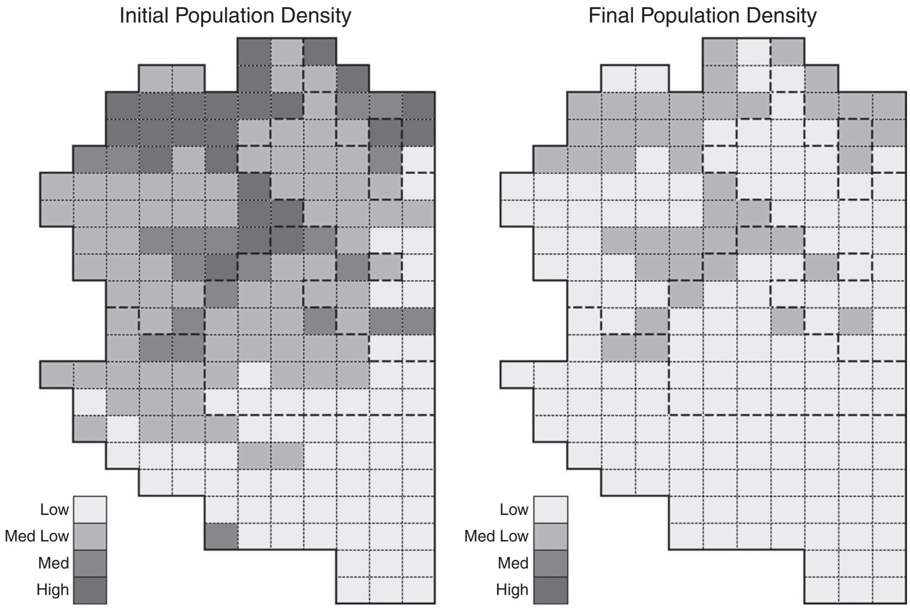

FIG. 17-1

Population density of feral buffalo (*Bubalus bubalis*) in Kakadu National Park, northern Australia, predicted by a lattice population model with 10 × 10 km grid cells. The left map shows densities prior to management, and the right map shows densities after a 10-year culling regime. The dashed lines delineate the land management zones, each subjected to different culling intensities.

clusters of cells, researchers were able to determine how to make the best use of limited logistical resources to minimize damage in the most environmentally and culturally sensitive areas of this large national park (Fig. 17-1).

Lattice models, by making use of a variety of data layers, can be arbitrarily complex. This modeling is useful because such models are naturally tailored to suit the type of data available, but it tends to limit the generalities that can be extracted from such computations; their results tend to be case specific. A more abstract but generalizable approach is to use cellular automata, in which just a few simple rules govern the interactions of individual cells. The fine-scale effects of habitat fragmentation on extinction risk can be examined (Oborny et al. 2005), and complex patterns that resemble real-world landscape features (e.g., banded vegetation in semi-arid savannas) often emerge from such cellular automata models (Rietkerk et al. 2004). Their consistent properties can be used to develop rules of thumb for managing habitat across large landscapes when few species-habitat data are available (With 1997). The challenge is to verify whether the generating mechanisms apply in real-world situations (Molofsky and Bever 2004).

Unlike metapopulation models that are based on discrete habitat patches, the resolution of the grid-based models is not based on the structure of the landscape. However, their resolution should be consistent with the biology of the species. Because population dynamics are simulated within each grid cell, there is an implicit assumption of the applicability of population processes at that scale. Hence, cells that are too small may not be suitable because the "population" in each cell may not have the properties of a biological population, and cells that are too large may not be appropriate because of the heterogeneity of the habitat within each cell.

Demographically Structured Metapopulation Models

Populations in which individuals differ in their contributions to population growth are structured, and these individuals can be classified by state (e.g., age, size, sex, developmental stage). When information is available on variation in vital rates, a tool commonly used to assess spatiotemporal changes in populations in large landscapes is matrix projection models (Caswell 2001). In general, structured models give a more detailed portrayal of metapopulation change through time than occupancy or time-series methods, and they can contribute to more targeted management questions because they identify the vital rates and specific states with the greatest influence on the population rate of change.

The probability of extinction and related viability metrics (e.g., risk of decline, probability of patch occupancy, population abundance) are usually estimated by Monte Carlo computer simulation. These models can take explicit account of demographic parameters (survival and fecundity), density dependence, environmental fluctuations, changes in the status of habitat, and the impact of infrequent, catastrophic events such as fire, cyclones, or disease epidemics (Akçakaya et al. 1999). In fragmented populations or species distributed over large landscapes, spatial correlation of environmental variation and dispersal are incorporated as a metapopulation model, with stage-structured patch-based populations being connected by movement rates defined according to a proportion of population size and distance between patches.

An issue prominent on the agenda of managers of wildlife populations in large landscapes is that of sustainable harvest. That is, what levels of off-take can a given wildlife population support, and importantly, what role do spatial refugia (e.g., reserves that are closed to hunting) play in offsetting harvest in other parts of a species' distributional range? Brook and Whitehead (2005) used a spatially structured demographic model to address this issue for magpie geese (*Anseranas semipalmata*), a species that was once found in abundance throughout eastern Australia, but is now restricted to the tropical wetlands of northern Australia and New Guinea. This model considered spatial and temporal variation in both habitat suitability and off-take. They showed that current levels of indigenous and recreational harvests could be supported over the long term in model systems that incorporated dispersal and spatial structure. Yet, if the same population size of geese were assumed to be distributed and harvested homogenously across the landscape, the species could not compensate sufficiently and was predicted to decline to extinction within decades.

As with most metapopulation models, the magpie goose model treated habitat patches (wetlands) as fixed, clearly defined units. However, in reality the definition of what constitutes habitat versus nonhabitat is often not clear cut. In such instances, habitat suitability models based on observed occurrences of species can facilitate definition of metapopulation spatial structure. One of the earlier examples of a metapopulation model in which patches were defined empirically, based on the distribution of suitable habitat, involved the California Gnatcatcher (*Polioptila c. californica*), a threatened species dependent on coastal sage scrub vegetation. The spatial structure of the metapopulation was based on a habitat suitability map (Fig. 17-2), which was predicted by a statistical habitat model (Akçakaya and Atwood 1997). This was based on sighting locations of observed pairs and maps of variables related to the species' habitat preferences, linked using a logistic generalized linear model. The RAMAS GIS software package (Akçakaya 2005) automates many of the steps required to achieve integration of landscape/vegetation maps, Habitat Suitability Index models, and metapopulation matrix projection models.

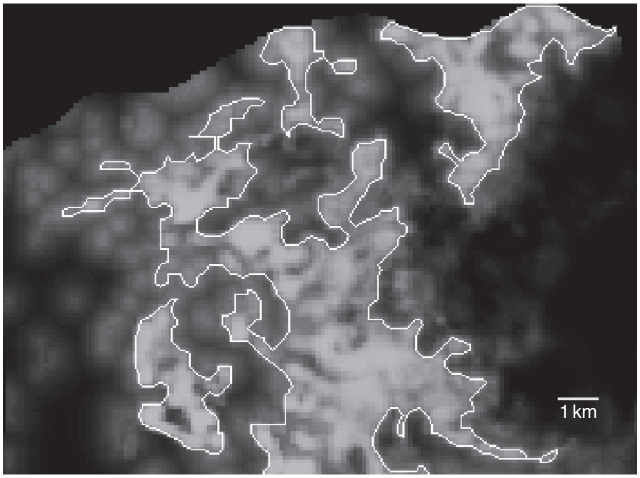

FIG. 17-2

Detail of the spatial structure of the habitat-based metapopulation model of the California Gnatcatcher. Shades of gray represent habitat suitability (the lighter the color, the higher the suitability), the white outlines are the outer borders of patches identified by the model based on a neighborhood distance parameter (Akçakaya and Atwood 1997). Cell (pixel) size of the underlying map is 100 meters. Each patch represents one population of the metapopulation model. The smallest patch in this section of the study area consists of 245 cells.

Recent work has demonstrated the value of incorporating the temporal dynamics of spatial data derived from landscape-scale vegetation models more directly into demographically structured metapopulation models of threatened species. Sharp-tailed grouse (*Tympanuchus phasianellus*) has declined in parts of its range due to loss of its steppe-grassland habitat. Its remaining habitat in Wisconsin is both fragmented and dynamic (i.e., the number, size, and distribution of patches change over time). The viability of this species was analyzed using a metapopulation model with dynamic spatial structure that was based on the predictions of a forest landscape model, which simulated landscape dynamics brought about by processes such as succession, disturbances, and silviculture (Akçakaya et al. 2004). The landscape component of the model predicted forest landscape dynamics in the form of a time series of raster maps. These maps were combined into a time series of patch structures, which formed the dynamic spatial structure of the metapopulation component. The results showed that the viability of this species 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 (Fig. 17-3).

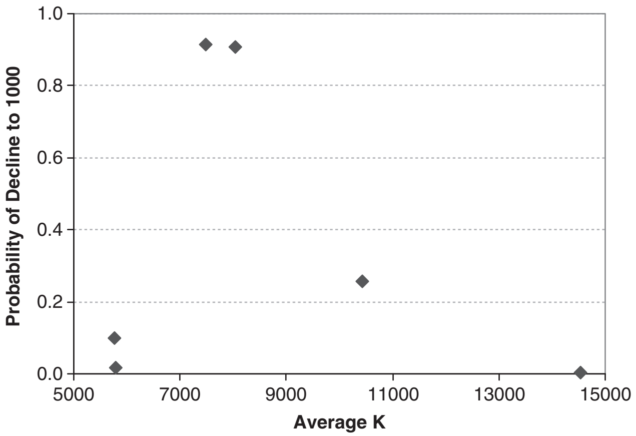

FIG. 17-3

Relationship between the amount of suitable habitat for the Sharp-tailed Grouse in the Wisconsin Pine Barrens region, USA (measured as total average carrying capacity) and viability (measured as risk of decline to 1000 individuals) for seven scenarios of forest management simulated by Akçakaya et al. (2004). Because of the interaction between landscape dynamics and the population dynamics of the species, the amount of habitat does not correctly predict the viability of the species.

Individual-Based Models

Individual-based models (IBMs) simulate the fate of each individual in a population, rather than cohorts, and like matrix-models, IBMs usually incorporate demographic and environmental stochasticity, habitat quality, and density dependence. The family of models IBMs entail has been extensively reviewed by Grimm (1999). The major advantage of IBMs is that individual heterogeneity is modeled explicitly. For instance, individuals may differ in the vital rates because of body condition, breeding status, the habitat quality within their exclusive home range, or because of their pedigree of inbreeding. These attributes reflect the relative contribution that each individual makes toward maintaining population viability, and can therefore be important to represent (White 2000). The caveats to developing IBMs are in the detailed data they demand, and the computational constraints of simulating large population sizes.

The IBM approach in population viability analysis is most frequently used for modeling small populations on the brink of extinction, which may be suffering from demographic failure, habitat loss, or inbreeding depression (e.g., Brito and Fernandez 2000, Lacy 2000). One interesting application of IBMs to populations in large landscapes was the simulation of an extinct predatory cat, *Panthera gombaszoegensis*, based on life history data of modern jaguars (*Panthera onca*). O'Regan et al. (2002) used the IBM software package VORTEX (Lacy 2000) to examine the size of refugial tracts of habitat that remained during repeated periods of intense glaciation in Pleistocene Europe that would have been sufficient to support viable and sufficiently interconnected populations.

An IBM approach more amenable to modeling populations in large landscapes is complex adaptive systems (CAS) modeling (Railsback 2001), which focuses on how the properties of aggregations of individuals can be determined by the characteristics and behavior of the individuals (e.g., habitat fidelity, food preferences, dispersal propensity, predator avoidance strategies). In essence, CAS approaches can translate ecological trends from individuals to landscape or population dynamics. This special class of IBMs is considered promising because unlike standard IBMs, no system-level responses are forced on the CAS (Elliot and Kiel 2002). Instead, ensembles of individuals within a spatially distributed population process information about their environment and modify their behavior according to a goal (Hraber and Milne 1997). The attractiveness of CAS is that it offers an alternative to parametric estimation approaches, which are often hampered by nonlinearity in data, unknown distributions, and problems associated with null data (e.g., determining why species do not forage in apparently suitable habitats). Complex adaptive system models are characterized by emergent responses (the ability to predict a wide range of realistic system-level attributes from a model in which individuals follow simple decision rules and regulatory responses) and can incorporate detailed spatial information and landscape-scale attributes linked to GIS. However, to date, the contribution of CAS to population management at the landscape-scale has been relatively minor, due at least in part to a lack of a validated "top-down" theoretical framework.

Selecting and Parameterizing a Model

Typically, the process of undertaking a population viability analysis goes through the following stages: (1) the identification of threatened species; (2) data collection (or collation) and analyses; (3) model formulation and construction; (4) simulations of the future fate of a population based on a range of potential threats (often projecting 50–100 years); and (5) the suggestion of possible remedial actions. Sensitivity analyses and the outcomes of various "what if?" scenarios are examined to evaluate different management options. Sensitivity analyses are also used to determine which parameters most strongly influence model predictions, and can be used to focus researchers' efforts on improving estimates of the most important variables (Caswell 2001).

The recent literature on viability analysis has emphasized the need to consider multiple working hypotheses and hence, more than one model (Burnham and Anderson 2002, Wintle et al. 2003). This operates at two levels:

1. When estimating the basic ecological attributes of a species, such as survival and reproductive rates or habitat suitability, one commonly uses a likelihood-based statistical model (e.g., generalized linear mixed effects model). It is critical at this stage to use robust methods of model selection that provide a measure of the strength of evidence for supporting models, such as information theoretic or iterative cross-validation methods to weight alternative models for multimodel inference. Alternatively, Bayesian statistical methods can be used to weight alternative model structures according to their posterior probabilities. The philosophical motivation for applying any of these weighting methods is that parameter estimates should be based on weighted estimates derived from all plausible models, using model weights to control for model selection uncertainty (Burnham and Anderson 2002).

2. When one is deciding on the choice of predictive models, the amount and type of available data provide a strong guide as to which method should be used. In general terms, simple approaches with few parameters, such as occupancy models, are easier to parameterize than more complex simulations, but less likely to fully encompass the range of potential factors that may influence the dynamics of a population. In instances in which there are sufficient data to parameterize a complex structure model, it may still be worthwhile also developing simpler approaches simultaneously. This acts as a check on the influence of model choice on predictions. It also makes transparent the structural generality/realism and parameter bias/precision trade-offs that are inevitable when deciding whether to use simple or complex models.

Irrespective of the model selection method used, it is important that parameter estimation is not divorced from biological intuition. For instance, some statistical data analysis techniques may produce estimates that are statistically valid but biologically implausible (such as obtaining negative multiple regression coefficients when estimating stage-specific fecundities; Akçakaya et al. 1999). In other cases the estimation of parameters will be prone to a lack of statistical power, and real trends may be overlooked. Because it is impossible to specify a general protocol to cover all such contingencies, the decision of when to reject or re-evaluate such estimates should be governed primarily by implicit knowledge of the particular species' biology.

Recent developments in wildlife population modeling have highlighted the value in combining the parameter estimation, model formulation, and population project stages. For instance, recent innovations in the development of Bayesian analysis using Markov Chain Monte Carlo (MCMC) allow the fitting of complex data to model, and include key aspects of individual and spatial heterogeneity (Clark et al. 2005). These hierarchical population dynamics models represent population structure as fixed stages and spatial strata, with differing levels of variability among individuals and groups.

Measurement errors and biases are inevitably incorporated into parameter estimates through imperfect data collection in the field (White 2000). For example, the commonly used Cormack-Jolly-Seber method of survival analysis associated with the mark-recapture techniques carries a set of implicit assumptions that, if violated, will lead to inexact parameter estimates (Lebreton et al. 1993). Due to imperfect data collection techniques, such measurement errors are usually impossible to eliminate. However, if there is a consistent bias when one technique of estimation is compared to another independent estimate, then the systematic bias can be calculated, and the value of the parameter(s) or counts can be adjusted accordingly (Akçakaya et al. 1999). Hierarchical Bayesian analysis is particularly robust to incomplete data.

FUTURE DIRECTIONS

There are many recent developments pertaining to PVA methods, especially on data analysis and estimation of demographic parameters (Holmes 2004, Dunham et al. 2006); model selection and multimodel inference (see previous section); prediction of habitat from occurrence data (Elith et al. 2006); detection and modeling of density dependence (Brook and Bradshaw 2006*b*); and estimating natural variability by removing variance due to measurement error and sampling variability (Dennis et al. 2006). We expect this trend to continue, with new quantitative methods providing more accurate and less biased estimation of parameters for various components of PVA, including habitat modeling, demographic modeling, and interactions among populations.

A major future direction is related to the incorporation of habitat and landscape dynamics discussed previously. Natural landscape dynamics and disturbance regimes interact with human land-use and large-scale human impacts to shape the landscape patterns that determine the spatial structure and dynamics of metapopulations. Ecological research in large landscapes that ignores the human element, or that includes it only as an implicit "extrinsic factor," is becoming increasingly regarded as unrealistic and artificial (Nyhus et al. 2002). The dynamics of coupled human and natural ecological systems are essential to understanding the ecology of populations and communities in large landscapes. In the future, we expect the development of much more explicit links between habitat-based PVA models and anthropogenic drivers of landscape change, such as climate change (including shifting bioclimatic envelopes; Keith et al. 2008) and human land use. These drivers in turn could be linked to models of human population dynamics and socioeconomics (Nyhus et al. 2002).

Closely related to the preceding developments are the challenges posed by compounded uncertainties, especially when the uncertain outputs of one model are used as inputs to the next model. In addition to new approaches for dealing with uncertainties, these challenges will also require new studies of validation, in which the available data are divided, with one set used for model development and the second set used for comparing with model predictions. This separation can be spatial or temporal. Spatial separation of populations in a large landscape can provide the opportunity to validate the generality and applicability of model predictions in the absence of long-term monitoring data. In one of the few validation studies involving PVA, Brook et al. (2000) validated PVA predictions of abundance and risks of decline, by temporally separating the available data, estimating the parameters from the first half of each data set and using the second half to evaluate model performance. They found that predictions were accurate; the risk of population decline closely matched observed outcomes; there was no significant bias; and population size projections did not differ significantly or importantly from reality. Further, the predictions of five software packages they tested were highly concordant. However, this study was based on a limited number of well-studied species; larger studies that attempt to validate PVA predictions would evaluate the reliability of models for different types of questions and available data and provide insights in terms of best modeling practices. Theoretical studies do suggest, however, that the reliability of population viability predictions degrades considerably as projection time frame exceeds a few generations, especially in highly variable systems. Nevertheless, the relative rankings of alternative management scenarios may be robust even when absolute predictions of risk are uncertain.

SUMMARY

We reviewed methods of population viability analysis (PVA) as applied to wildlife populations in large landscapes. For these populations, viability analysis requires careful consideration of the issues of spatial heterogeneity and scaling of ecological processes, habitat connectedness (including "permeability of the intervening matrix"), and temporal dynamics of the landscape. Spatially structured models used for large-scale PVA include occupancy models, grid-based lattice models, demographically structured metapopulation models, and individual-based models. We discussed the assumptions and limitations of model types and the context within which each is more appropriate. Population viability analyses in large landscapes often require the definition of distinct subpopulations, which in turn depend critically on the spatial scale of, and barriers to, dispersal in relation to the distribution of suitable habitat. Another important factor is the effect of landscape dynamics on the temporal variability of the habitat, and hence on the dynamics of the wildlife populations. Viability of species in dynamic landscapes depends on the interaction between landscape change (the pattern, scale, rate, and direction of landscape changes in size, structure, and quality) and the species' ecology (its ability to disperse between and grow in the habitat patches or make use of the matrix). Spatial separation of populations can also provide the opportunity to validate the generality and applicability of model predictions in the absence of long-term monitoring data.

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