

Population Viability

as a Measure of Forest Sustainability

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Abstract—Many forest managers work to balance timber production with protection of ecological processes and other nontimber values. The preservation of biodiversity is an important nontimber value. When a suite of management options is being developed, it is difficult to estimate quantitatively the impact of the various scenarios on biodiversity. We suggest population viability analysis (PVA) as a tool for estimating the quantitative impact of landscape modifications on species. Using a habitat-based approach to PVA, we examine the potential effects of five management alternatives on the chestnut-sided warbler (*Dendroica pensylvanica*), a management-indicator species, on the Cherokee National Forest in Tennessee. This analysis shows that population size is positively correlated with disturbance. It also appears that without active management, this species, which is dependent upon early successional forests, may not find enough suitable habitats to maintain viable populations over the next 50 years. Although habitat-based PVA is demonstrated here for a single species, it has been modified to assess large biota. Habitat-based PVA is a useful tool for those who must assess the potential impact of landscape modification on biodiversity.

INTRODUCTION

During the late 1800s and early 1900s, the forests of the Southern United States were overexploited and mismanaged in ways that resulted in depletion of timber resources, extensive erosion, degradation of water quality, and negative impacts on wildlife habitat and wildlife populations. The latter half of the 20th century saw the emergence of new attitudes regarding land use by private and public landowners. Legislation such as the Multiple-Use Sustained-Yield Act of 1960 and the National Forest Management Act of 1976 requires that national forests be managed for both timber and nontimber values. Today, forest managers are beginning to work to achieve ecological sustainability on both public and private lands (Kohm and Franklin 1997). Pursuit of ecological sustainability includes efforts to maintain ecosystem functions and processes, timber production, and nontimber values. Biological diversity, or biodiversity, is an important nontimber value. Biodiversity is diversity at the genetic, species, landscape, and ecosystem level (Noss and Cooperrider 1994). However, it can be difficult to assess the success of management for biodiversity (Botkin and Talbot 1992). Managing for biodiversity requires the development of strategies for monitoring the flora and fauna of the area in question (Lindenmayer and others 1999). Only a few researchers have described organized approaches to planning for biodiversity as an objective of multiple-use management (Kuusipalo and Kangas 1994, Millar and others 1990, Probst and Crow 1991).

Management to conserve biodiversity or to avoid species extinction is generally addressed at the scale of a species geographic range, which may extend across many political boundaries, ecoregions, or even continents. Species that are widespread and abundant are generally of little management concern, although nonnatives and

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pests are notable exceptions to this rule. Most rare species are of management concern, however, and since most managers work on a spatial scale that is small relative to a species global distribution, preserving biodiversity is really a matter of preserving populations. Small populations are subject to environmental stochasticity and many other uncertainties and are consequently more at risk of extinction. Thus, if populations are to persist, they must be adequately large (Menges 1990, Pimm and others 1988).

It is generally acknowledged that a greater diversity of habitat types is positively correlated with greater biodiversity. Forest management generally affects the composition and spatial arrangement of forest stands at the landscape scale. Different management practices can produce profoundly different habitat conditions. Industrial forest lands, for example, may support large (> 50 ha) even-aged stands of trees of a single species; e.g., loblolly pine (*Pinus taeda* L.). Biodiversity in these managed forests can be enhanced by maintaining a diversity of stand-age classes and stand-size classes across the landscape. Other silvicultural practices that modify forest habitat conditions include thinning and prescribed burning. It can be difficult to predict the consequences when habitat conditions are modified over large areas. For this reason, tools that assess landscape change can be particularly valuable. The use of spatially explicit habitat models is one such tool (Dunning and others 1995).

Population viability analysis (PVA) has been used to predict the likelihood that a population of a single species will persist over a given time period (Boyce 1992, Nunnery and Campbell 1993, Soulé 1987). The relative merits of the criteria used in such analyses have been discussed elsewhere (Mace and Lande 1991). Early PVA employed deterministic models that examined the management of endangered species and relied solely on demographic analyses (Miller and Botkin 1974). Later, population models that incorporated demographic and environmental stochasticity were developed (Menges 1990; Shaffer 1981, 1983). Since these models account for a portion of the stochastic events characteristic of small populations, this marked a dramatic improvement in PVA. In 1986, the conceptual framework of PVA was broadened to include a comprehensive examination of factors that can affect the persistence of populations (Gilpin and Soulé 1986). Population persistence is subject to

variation arising from several sources, including stochastic, demographic, temporal, spatial, individual, and other processes (White 2000). One challenge associated with the use of PVA is an accurate estimate of the variation induced by such processes. A number of researchers have studied parameter estimation and its influence on model performance (Akçakaya and others 1997, Burgman and others 1993, Conroy and others 1995, Dennis and others 1991, Groom and Pascual 1998, Ludwig 1999, Taylor 1995, White 2000).

One outcome of quantifying population persistence is the concept of the minimum viable population size (MVP) (Harris and others 1987). An MVP is an estimate of the minimum number of individuals required to constitute a population that can persist for a given time period. There has been considerable debate about the characteristics of MVPs (Harris and others 1987, Henriksen 1997, Thomas 1990). Many aspects of species biology must be considered when workers attempt to determine what the MVP is, and these aspects will vary across taxa and with circumstances, e.g., genetic variability, mating system, reproductive power. PVA has continued to evolve as a conservation tool and now includes demographic, genetic, and spatially explicit models (Beissinger and McCullough 2002, Young and Clarke 2000). The various roles played by PVA have been summarized by Burgman and Possingham (2000).

The most common approach to PVA is to model species demography. This usually occurs when species abundance is relatively low, and there are relatively few populations. Demographic PVA has been conducted for dozens of species, and these analyses have ranged from simple population projections to spatially explicit, individual-based models that include heterogeneous landscapes and age-specific demographics (Beissinger and Westphal 1998). One especially interesting aspect of demography is sensitivity analysis (Crouse and others 1987, Mills and others 1999), which can be used to determine which demographic parameter, e.g., juvenile survival, birth rate, has the greatest impact on the population growth rate. Managers can plan their actions in accordance with such analysis, but the use of this method does not guarantee success.

When a single population is under consideration, demographic model development is relatively straightforward but is affected by the type and quantity of data under consideration (Morris and others 1999). When the spatial scale

is sufficiently large or when multiple populations are under consideration, a new approach may be useful. For example, one can include a spatial component in the model. This component can be explicit (Lindenmayer and Possingham 1996) or nonexplicit (Hanski and others 1996). Both of these approaches have merits, and both are consistent with the use of PVA to make specific spatial decisions. This makes PVA an extremely valuable conservation and management tool. However, a major drawback of spatially explicit models is that it takes additional data to construct and run them. Also, the use of additional model parameters may negatively impact predictability (Ruckelshaus and others 1997). It is up to the modeler to decide whether a more complex model, which typically represents a more biologically realistic depiction, is preferable to a simpler model that requires less time and effort to construct.

Because count data are easily collected and relatively inexpensive, they are commonly available to land managers. Count data can be used to construct simple time-series models for the projection of population estimates (e.g., Boyce and Miller 1985, Dennis and others 1991). It is important to know whether a population trajectory is based on data for a single population or for several populations. Because a species may be declining in some populations while increasing in others, it can be very helpful to incorporate spatial structure into population models (Stacey and Taper 1992, White 2000). Another factor to be considered is the adequacy of the time span employed. Morris and others (1999) suggest that a minimum of 10 years be used. However, even when a long-term dataset, e.g., 26 years, is employed, conclusions about population persistence can become outdated quickly when populations change abruptly (Boyce 2001, Dennis and others 1991). Finally, although time-series models are useful in determining population trajectories, they offer no insight into the processes driving the population decline.

Another approach to PVA is to examine the ecological factors associated with population decline or population stochasticity. Loss or degradation of habitat is the most significant threat facing species (Pimm and Gilpin 1989, Wilcox and Murphy 1985). Habitat loss is listed as a significant threat for 82 percent of endangered bird species (Temple 1986). Other factors that can reduce the viability of a population include predators, nonnative species, parasites, and disease. However, ecological variables are

rarely addressed in PVA because of the difficulty of collecting the necessary data and incorporating them into analyses (Boyce 1992).

In response to criticism surrounding the use of only demographic-based PVA for land management decisions (Harrison 1994, Taylor 1995), researchers attempted to develop a habitat-based approach (Roloff and Haufler 1997, White and others 1997). Two approaches have been developed, and both are based upon concepts rooted in community and population ecology. Community ecologists have developed the concept of minimum area requirements, while population biologists have emphasized minimum population size (Soulé 1987). Both approaches quantify the habitat available in a given landscape and then estimate the sustainable population size. Both assess a landscape's potential (the amount of suitable habitat available for the target species) but differ in their assessment of the detail of data required to conduct risk analysis. White and others (1997) use general habitat relationships to determine habitat suitability, while Roloff and Haufler (1997) use an empirically derived, spatially explicit habitat model. Both approaches utilize presence and absence data, which can be collected with considerably less time and effort than demographic data.

The use of PVA is important in mitigating the negative effects of landscape change on biodiversity (Burgman and others 1993). Habitat loss and fragmentation continue to challenge conservationists. PVA models have evaluated the impacts of habitat fragmentation or loss (Lindenmayer and Possingham 1994, McCarthy and Lindenmayer 1999, Noon and McKelvey 1996), established area requirements (Goldingay and Possingham 1995), and aided in optimizing the design of nature reserves (Burgman and others 1993, Lindenmayer and Possingham 1994). However, PVA has limitations that should be recognized (McCarthy and others 1996, Taylor 1995). The most useful products of a PVA may not be the absolute numbers or statistics generated, but rather the relative values generated under various management scenarios (Boyce 1992). Relative impacts of various management scenarios have been assessed for a handful of species (Drechsler 1998, Haig and others 1993, Lindenmayer and Possingham 1996, Pfab and Witkowski 2000). In the present case study, we use habitat-based PVA to examine the impact of various management scenarios on the viability of forest songbirds.

CASE STUDY

The management of public lands is a central element of national environmental policy in the United States. The management practices employed on public lands today are an outgrowth of past practices, growing awareness of ecosystem importance, and conflicts over various issues, e.g., wilderness vs. timber production. Attempts to resolve these issues can be expensive for all parties concerned. For example, the USDA Forest Service spends over \$5 million annually on lawsuits regarding proposed sales of timber on land it manages (U.S. Department of Agriculture, Forest Service 1997). One contentious issue is the role of timber management in the management of our national forests. Impacts on native flora and fauna have been cited as reasons for limiting timber harvests (Harwood 1997). Many studies have examined the impact of forest management on a variety of plant and animal groups. In this study, we focus on impacts on forest songbirds.

Most studies associated with bird communities and timber management examined the impact of a particular treatment on community structure. This is done by examining the bird community before and after harvests. Most such studies have concluded some species are negatively impacted by timber harvesting and that other species benefit from it (Thompson and others 1992). From a management perspective, this suggests that timber harvesting may be a viable option for the management of habitat for some songbirds.

Natural disturbance has always shaped forest communities; anthropogenic disturbance, e.g., silviculture, has had an important role in shaping North American forest communities for the past 200 years (Smith and others 1996). The frequency, intensity, and type of disturbance affect forest structure and composition. Bird communities change dramatically in response to these changes in habitat conditions (Newbold 1996).

We considered two silvicultural methods in this case study: even-aged and uneven-aged timber harvesting. On the Cherokee National Forest (CNF), recent even-aged management consists of relatively small clearcuts averaging 10 ha in area. Clearcutting has been the preferred regeneration system on the CNF for the past 30 years. However, because of public opposition to clearcutting, uneven-aged management may predominate in the future. The CNF uses group-selection cuts that result in a forest that is structurally diverse at the understory, midstory, and canopy levels. This approach results in forests

that have structural attributes similar to those of old-growth forests (Annand and Thompson 1997, Thompson 1993). However, uneven-aged harvesting is a relatively recent silvicultural approach and, consequently, few studies have evaluated its potential as a management tool (Annand and Thompson 1997, King and others 2001, Twedt and others 2001). The goals of this case study are to assess the effects of various management alternatives on the viability of the chestnut-sided warbler (*Dendroica pensylvanica*) (CSWA), a forest songbird. To achieve this, we ask three basic questions:

1. Are current harvest levels adequate to support viable populations of CSWAs?
2. What is the impact of natural disturbance in providing habitat for the CSWA?
3. What timber harvesting strategy best promotes the viability of the CSWA on the CNF?

We show how a habitat-based PVA can be used to assess the impact of various management scenarios on CSWA, a species that is typically associated with early succession forests.

METHODS

Point-count data collected in the CNF during the 1992–96 breeding seasons were used to construct a habitat model. Standardized avian census methods were employed (Hamel and others 1996). Habitat variables were derived from the Forest Service's Continuous Inventory of Stand Conditions (CISC) database and the Southern Appalachian Assessment database. Variables included forest type, condition class, stand age, site index, and elevation (table 26.1). Both databases exist in a Geographic Information System, and our analysis was conducted at a pixel resolution of 30 m², which is a scale appropriate for our target species. We used stepwise logistic regression (PROC LOGISTIC) (SAS/STAT 1990) with a $P < 0.10$ level to build a habitat model to predict the occurrence of CSWAs. The habitat model was then applied back onto the CNF, creating a probability surface that reflected the likelihood of occurrence of breeding territories ranging from zero to one. To estimate the amount of suitable habitat on the CNF, we multiplied the likelihood of occurrence for each stand by that stand's acreage. The products are similar to the habitat units (HU) in a Habitat Suitability Index model (Schroeder 1983), which for this case study, is equal to 1 ha of suitable habitat. To convert the products into an estimate of the potential to

Table 26.1—Habitat variables and descriptions used to construct chestnut-sided warbler model

Habitat variable	Description	Range
Age (years)	Current age of stand	0 – 172
Forest type		
Yellow pine	Yellow pine forest	0 – 1
White pine-hemlock	White pine or hemlock forest	0 – 1
Cove hardwood	Cove hardwood forest	0 – 1
Northern hardwood	Northern hardwood forest	0 – 1
Mixed hardwood-pine	Mixed hardwood and pine forests	0 – 1
Oak-hickory	Oak-hickory forest	0 – 1
Stand-condition class		
Seed	Seedling-sapling	0 – 1
Pole	Poletimber	0 – 1
Saw	Sawtimber	0 – 1
Site index (feet)		
Site index 1	Site potential, dominant tree height in 50 years	4 – 130
Site index 2	Site index < 70	0 – 1
Site index 3	70 < site index < 80	0 – 1
Site index 4	80 < site index < 110	0 – 1
Elevation (m)		
Elevation 1	Elevation	231 – 1530
Elevation 2	Elevation < 475	0 – 1
Elevation 3	475 < elevation < 872	0 – 1
Elevation 4	Elevation > 872	0 – 1

support a given breeding population, we summed the products across the study area and multiplied the total by the average breeding density of CSWA from Hamel (1992). We used a minimum viable population size of 250 breeding pairs, a very optimistic estimate, as the critical threshold below which the species would not persist. To avoid overestimation of available habitat on the strength of marginal probabilities of occurrence, we stipulated that habitat would not be considered suitable where the probability of occurrence was < 75 percent. Habitat patches that were less than one territory in size were not considered suitable.

In this exercise, we projected figures from CISC databases 60 years into the future. This was accomplished by using a SAS-based forest model to simulate even-aged and uneven-aged timber harvests. The management alternatives developed varied with forest type, total area harvested per 10-year interval, relative proportion of even-aged to uneven-aged harvesting (area basis), group size, and intensity of harvest. Specific variation of

intensities and harvesting methods were based on past harvesting practices and expert opinion of the district silviculturists. Since our target species is associated with early succession habitat, we also considered the rate at which forests were restoring themselves naturally. Consequently, we modeled five natural disturbances on the basis of existing literature and historical averages for this region. Natural disturbances included fire, ice, wind, southern pine beetle (*Dendroctonus frontalis* Zimmermann), and hemlock woolly adelgid (*Adelges tsugae* Annand). Each was assigned randomly to forest stands that could be affected by the type of disturbance; e.g., southern pine beetle did not impact northern hardwood stands. For each simulation, virtual forests were updated every 10 years.

Five scenarios were simulated, each with a different intensity of disturbance: no timber harvesting or natural disturbance, no harvesting but natural disturbance, harvesting at expected level (based on recent average harvests on the

CNF), 200 percent of expected harvest, and harvesting at 300-percent expected levels. These scenarios offered a range of disturbance intensities and allowed us to assess the impact of various management practices compared to natural disturbance rates. Using the ArcView Spatial Analyst extension (Environmental Systems Research Institute 1996), we calculated the area of each habitat patch for each simulation. Number of habitat units was calculated for each 10-year interval and so that the habitat potentials for the disturbance scenarios could be compared easily.

We also conducted sensitivity analysis on the habitat variables to test their relative importance. Each forest simulation was run repeatedly, with systematic manipulation of input variables at each harvest level and at levels 30 percent above and below each harvest level. The OPTEX procedure (SAS 1990) was used to identify a subset of variable settings, and this reduced the number of iterations necessary. The response of total HUs to each habitat variable was then tested using the general linear model procedure (PROC GLM) (SAS 1990). Sensitivity analysis quantified the importance of each variable independent of the relative abundance of each forest type. This approach was also used to compare the influence of management alternatives across forest types.

RESULTS

The CSWA is relatively uncommon in our study area, occurring on 14 percent of census points. The CSWA model included positive associations with elevation, seedling and/or sapling condition class, site index, and several forest types (table 26.1). Variation explained (indicated by max-rescaled R-square) was 0.6484. The correct classification percentage (concordance) was 95.6, which is relatively high. The Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989) indicated that the fit of the data was acceptable at $P > 0.05$. The CSWA model indicated that preferred habitat consisted of young productive forests at elevations > 1000 m.

Characteristics of high-quality habitat varied across the landscape, with northern hardwoods providing the greatest breeding opportunities (662 HUs), followed by oak-hickory (520 HUs), mixed pine-hardwood (113 HUs), yellow pine (48 HUs), and hemlock-white pine (34 HUs). CSWA habitat was positively associated with most types of disturbance, including (in order of descending importance) area of even-aged harvesting in oak-hickory, area of disturbance by ice and or wind,

area of even-aged harvesting in cove hardwoods, area of uneven-aged harvesting in oak-hickory, and area of even-aged harvesting in mixed pine-hardwoods. Disturbance by fire, southern pine beetle, and hemlock woolly adelgid were not related to habitat availability for CSWA. Not surprisingly, the strongest negative association with habitat availability was the association with forest age. Sensitivity analysis indicated that most forms of disturbance were extremely important in generating suitable habitat. Ice and/or wind disturbance was the only natural disturbances that were of much importance, however.

At expected levels of harvesting, the amount of suitable CSWA habitat increased slightly (8 percent) from 1993 to 2053. Based on an average breeding density of 11.9 breeding pairs per 40 ha (Hamel 1992), the initial landscape in 1993 could support approximately 416 breeding pairs. Based on the various disturbance scenarios, the landscapes could support from 250 to 790 breeding pairs in 2053, with suitable habitat being positively correlated with disturbance (fig. 26.1). Thus all disturbance scenarios considered provided adequate habitat to ensure viability (MVP = 250). In the 300-percent harvesting scenario, the number of HUs available increased dramatically the first three decades and declined over the last two decades. The decline in suitable habitat resulted from maturation of trees in the previously harvested areas and a lack of stands suitable for harvesting in the latter years of this simulation.

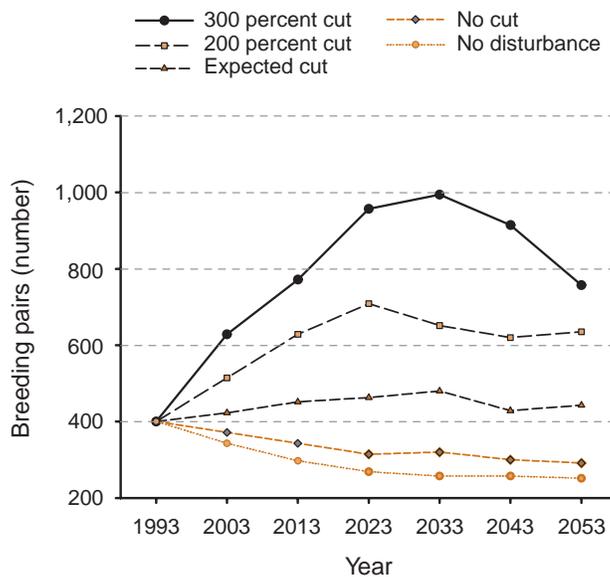


Figure 26.1—Habitat potential for the chestnut-sided warbler on the Cherokee National Forest under five management alternatives over a 60-year time horizon.

DISCUSSION

Disturbance is vital to the maintenance of habitat for CSWA. However, sensitivity analysis suggests that natural disturbance contributes relatively little to the creation of habitat suitable for CSWA on the CNF. If viable populations of CSWA are to be maintained, it may be necessary to create additional suitable habitat by means of active management.

Only habitat variables found in the CISC database were employed in this study. The virtual forests regenerated by timber harvesting were very similar, in terms of CISC variables, to forests regenerated by natural disturbance. For example, simulated clearcuts and wildfires reset condition class and age to identical values. In actual systems, disturbances of these types are likely to produce dissimilar biological results. Schulte and Niemi (1998) found that key habitat characteristics of logged and burned sites differed significantly, and that this resulted in avian richness and abundance. Similarly, there were structural differences between forests that had been disturbed by tornadoes and those that had been clearcut (Newbold 1996). Again there were differences in avian community composition, but diversity did not vary with source of disturbance in this instance. Natural disturbance should be incorporated into habitat models systems in which it can play a significant role.

Habitat for CSWA can easily be created through forest management. It is possible to manage for species associated with late-successional forest by allowing forest stands to age, but it may take decades for high-quality, late-successional habitat to develop. It may be necessary to use silvicultural treatments to promote development of structural characteristics, e.g., snags, cavities, or den trees, important to species dependent on this habitat. The challenge for managers is to provide the balance of habitat types, seral stages, and landscape configurations that is most suitable for the desired diversity of species.

The results of this particular study are relatively clear with respect to CSWAs, as the management alternatives evaluated were distinct and only the intensity of harvesting varied among simulations. Because the approach we employed is spatially explicit, we could have compared the relative effects of several scenarios while maintaining consistent harvest volume. A spatially explicit approach can also be used to assess the

effects of several different landscape configurations. Researchers have developed decisionmaking tools for assessing scenario outcomes in studies that yield results that are less clear (Burgman 2000, Drechsler 2000).

Several potentially conflicting ecological, social, and economic factors must be accounted for when planners attempt to formulate the best land use plan for a tract of land. Various pressures are causing researchers, managers, and the general public to devote more attention to the problem of preserving biodiversity (Kuusipalo and Kangas 1994, Lindenmayer and others 1999). The preservation of biodiversity implies the maintenance of viable populations of all species deemed desirable. While PVA is a useful management tool, it is not possible to conduct intensive analyses for each species within the area of interest. It may be necessary to conduct analyses only for indicator species. The use of indicator species is meant to make it possible to estimate the responses of multiple species to a variety of alternatives without addressing the requirements of each species individually. The appropriateness, advantages, and disadvantages of using indicator species in planning for sustainable forestry has been addressed elsewhere (Lindenmayer and others 1999).

There are several criticisms of demographic-based PVAs (Harrison 1994, Taylor 1995). However, a recent retrospective analysis of the predictive accuracy of PVAs clearly demonstrated their value as a management tool (Brook and others 2000). One study that made use of spatially explicit models and specific management plans was conducted by Liu and others (1995) who examined the potential effects of several management practices on Bachman's sparrow (*Aimophila aestivalis*). This species breeds in open, mature pine stands, which are also being managed for the endangered red-cockaded woodpecker [*Picoides borealis* (Vieillot)]. In their analysis, Liu and others (1995) considered several aspects of management, including thinning, burning, and harvesting. Results indicated that certain harvesting practices, such as clustered harvesting, produced a landscape more favorable to juvenile dispersal and subsequent survival. Age-specific thinning and burning of some stands made them suitable as habitat at an earlier age. One of the important findings of this study is that Bachman's sparrow and red-cockaded woodpecker apparently require very different management, although both species are associated with mature pine stands.

In this system, the threat of habitat resulting from stochastic events is relatively high (Dunning and Watts 1991), which increases the likelihood of extinction because population size is small (Shaffer and Samson 1985).

Another excellent analysis of forest management and population viability was Lindenmayer and Possingham's (1996) study of the endangered Leadbeater's possum (*Gymnobelideus leadbeateri*). This species is associated with ash forests (*Eucalyptus*) in Australia and prefers to nest in large trees that are several hundred years old (Lindenmayer and others 1991). The majority of suitable habitat for this species is designated for timber harvesting, which makes future viability of the species quite uncertain. Using ALEX, a computer program for PVA (Possingham and Davies 1995), Lindenmayer and Possingham (1996) attempted to address some of the issues related to the conservation needs of Leadbeater's possum. They increased the usefulness of their PVA model by incorporating a submodel to account for the spatial and temporal variation in habitat quality. Results indicated that spatial arrangement and size of habitat were important factors in extinction risk. Landscapes that contain fewer but larger patches of habitat are often more suitable for species that depend on old-growth forest, but Lindenmayer and Possingham found that landscapes that contain more and smaller habitat patches are more satisfactory for Leadbeater's possum.

A possible objection to the use of habitat models is they are usually developed for a single species. Using some sort of indicator species may alleviate some, but not all, of the concerns associated with the use of a single nonindicator species. One option is to develop these models for a suite of species, thus capturing the diverse ecological requirements of most of the biota in question. White and others (1997) developed a habitat-based approach to risk assessment; they attempted to quantify the risk of landscape change for all terrestrial vertebrates in a particular county. Landscape changes were largely socioeconomic in origin and thus partly subject to control by county-level zoning restrictions. The first steps in determining the potential impact on biodiversity were to estimate area requirements of each individual species and then to determine the quantity of each habitat type. Six possible future landscapes were generated, with varying amounts of each habitat

type in each scenario. Because this was done in a spatially explicit framework, patch size could be determined, and this made it possible to estimate carrying capacity of each patch for each species. Species richness was calculated for each landscape plan. Results indicated that some land use plans were considerably more detrimental to biodiversity than others. While this approach lacks the precision of a single-species habitat model, it undoubtedly requires less data than many others, and this can make it a viable option when workers are attempting to assess the effects on the entire biota.

SUMMARY

Our study illustrates the use of PVA to assess the relative merits of various management alternatives, especially when lack of time or money makes it impractical to collect demographic data. If natural disturbance continues at historic rates for the next 50 years, early successional habitat may not be created rapidly enough to sustain a viable population of CSWA. Managers may have to actively disturb the landscape to provide suitable habitat for species that utilize early successional habitat and are less abundant than CSWA. Species associated with late-succession habitat are likely to see available habitat continue to increase unless the frequency and intensity of disturbance increase beyond normal historical levels. Managers must balance the need for additional habitat for early successional species with the need to maintain suitable habitat for late-successional species.

The approach we have outlined is firmly based on established ecological principles and is well suited for meeting management objectives. Two factors that strongly influence population viability are area of suitable habitat (Laurance 1991) and population size (Pimm and others 1988). Demographic models may be too resource intensive for use in assessing the impact of future landscape changes on an entire biota. Habitat-based PVA does require sound habitat models, and thus an appropriate set of habitat variables as well as reliable distribution data on the target species (Roloff and Haufler 1996). Other concerns related to the use of habitat models have been addressed elsewhere (Beutel and others 1999, Karl and others 2000). We advocate the use of habitat-based PVA in management planning where it is applicable.

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LITERATURE CITED

- Akcakaya, H.R.; Burgman, M.A.; Ginzburg, L.R. 1997. Applied population ecology. Setauket, NY: Applied Biomathematics. 285 p.
- Annand, E.M.; Thompson, F.R., III. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management*. 61: 159–171.
- Beissinger, S.R.; McCullough, D.R., eds. 2002. Population viability analysis. Chicago: University of Chicago Press. 562 p.
- Bessinger, S.R.; Westphal, M.I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*. 62: 821–841.
- Beutel, T.S.; Beeton, R.J.S.; Baxter, G.S. 1999. Building better wildlife-habitat models. *Ecography*. 22: 219.
- Botkin, D.B.; Talbot, L.M. 1992. Biological diversity and forests. In: Sharma, N., ed. Contemporary issues in forest management: policy implications. Washington, DC: The World Bank: 47–74.
- Boyce, M.S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics*. 23: 481–506.
- Boyce, M.S. 2001. Population viability analysis: development, interpretation, and application. In: Shenk, T.M.; Franklin, A.B., eds. Modeling in natural resource management. Washington, DC: Island Press. 223 p.
- Boyce, M.S.; Miller, R.S. 1985. Ten-year periodicity in whooping crane census. *Auk*. 102: 658–660.
- Brook, B.W.; O'Grady, J.J.; Chapman, A.P. [and others]. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature*. 404: 385–387.
- Burgman, M.A. 2000. Population viability analysis for bird conservation: prediction, heuristics, monitoring and psychology. *Emu*. 100: 347–353.
- Burgman, M.A.; Ferson, S.; Akcakaya, H.R. 1993. Risk assessment in conservation biology. London, United Kingdom: Chapman and Hall. 314 p.
- Burgman, M.A.; Possingham, H.P. 2000. Population viability analysis for conservation: the good, the bad and the undescribed. In: Young, A.C.; Clarke, G.M., eds. Genetics, demography and viability of fragmented populations. Cambridge, United Kingdom: Cambridge University Press: 97–112.
- Conroy, M.J.; Cohen, Y.; James, F.C. [and others]. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications*. 5: 17–19.
- Crouse, D.T.; Crowder, L.B.; Caswell, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*. 68: 1412–1423.
- Dennis, B.; Munholland, P.L.; Scott, J.M. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*. 61: 115–143.
- Drechsler, M. 1998. Spatial conservation management of the orange-bellied parrot *Neophema chrysogaster*. *Biological Conservation*. 84: 283–292.
- Drechsler, M. 2000. A model-based decision aid for species protection under uncertainty. *Biological Conservation*. 94: 23–30.
- Dunning, J.B.; Stewart, D.J.; Danielson, B.J. [and others]. 1995. Spatially-explicit population models: current forms and future uses. *Ecological Applications*. 5: 3–11.
- Dunning, J.B.; Watts, B.D. 1990. Habitat occupancy by Bachman's sparrow in the Francis Marion National Forest before and after Hurricane Hugo. *Auk*. 108: 723–725.
- Gilpin, M.; Soulé, M.E. 1986. Minimum viable populations: processes of species extinction. In: Soulé, M.E., ed. Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer: 19–34.
- Goldingay, R.; Possingham, H. 1995. Area requirements for viable populations of the Australian gliding marsupial *Petaurus australis*. *Biological Conservation*. 73: 161–167.
- Groom, M.J.; Pascual, M.A. 1998. The analysis of population persistence: an outlook on the practice of viability analysis. In: Fielder, P.L.; Kareiva, P.M., eds. Conservation biology for the coming decade. New York: Chapman and Hall: 4–28.
- Haig, S.M.; Belthoff, J.R.; Allen, D.H. 1993. Population viability analysis for a small population of red-cockaded woodpeckers and an evaluation of enhancement strategies. *Conservation Biology*. 7: 289–301.
- Hamel, P.B. 1992. Land manager's guide to the birds of the Southeast. Chapel Hill, NC: The Nature Conservancy, Southeastern Region. 437 p.
- Hamel, P.B.; Smith, W.P.; Twedt, D.J. [and others]. 1996. A land manager's guide to point counts of birds in the Southeast. Gen. Tech. Rep. SO-120. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 39 p.
- Hanski, I.A.; Moilanen, A.; Pakkala, T. 1996. The quantitative extinction function model and persistence of an endangered butterfly metapopulation. *Conservation Biology*. 10: 578–590.
- Harris, R.B.; Shaffer, M.L.; Maguire, L.A. 1987. Sample sizes for minimum viable population estimation. *Conservation Biology*. 1: 72–76.
- Harrison, S. 1994. Metapopulations and conservation. In: Edwards, P.J.; May, R.M.; Webb, N.R., eds. Large-scale ecology and conservation biology. London, England: Blackwell Scientific Publishing: 111–128.
- Harwood, J. 1997. The Tennessee sustainable forest management act of 1997—an overview. In: Jenkins, R.; McDonald, S., eds. The Tennes-Sierran. April: 1.
- Henriksen, G. 1997. A scientific examination and critique of minimum viable population size. *Fauna Norvegica*. (A)18: 33–41.
- Hosmer, D.W.; Lemeshow, S. 1989. Applied logistic regression. New York: John Wiley. 290 p.
- Karl, J.W.; Wright, N.M.; Heglund, P.J. [and others]. 2000. Sensitivity to species habitat-relationship model performance to factors of scale. *Ecological Applications*. 10: 1690–1705.

- Kohm, K.; Franklin, J.F. 1997. *Forestry in the 21st century*. Covelo, CA: Island Press. 475 p.
- Kuusipalo, J.; Kangas, J. 1994. Managing biodiversity in a forestry environment. *Conservation Biology*. 8: 450–460.
- Laurance, W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology*. 5: 79–89.
- Lindenmayer, D.B.; Cunningham, R.B.; Tanton, M.T. [and others]. 1991. The characteristics of hollow-bearing trees inhabited by arboreal marsupials in the montane ash forest of the central highlands of Victoria, South-east Australia. *Forest Ecology and Management*. 40: 289–308.
- Lindenmayer, D.B.; Margules, C.R.; Botkin, D.B. 1999. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology*. 14: 941–950.
- Lindenmayer, D.B.; Possingham, H.P. 1994. The risk of extinction: ranking management options for Leadbeater's possum using population viability analysis. Canberra, Australia: The Australian National University, Centre for Resource and Environmental Studies. 204 p.
- Lindenmayer, D.B.; Possingham, H.P. 1996. Ranking conservation and timber management options for Leadbeater's possum in Southeastern Australia using population viability analysis. *Conservation Biology*. 10: 235–251.
- Liu, J.; Dunning, J.B., Jr.; Pulliam, H.R. 1995. Potential effects of a forest management plan on Bachman's sparrow (*Aimophila aestivalis*): lining a spatially explicit model with GIS. *Conservation Biology*. 9: 62–75.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology*. 80: 298–310.
- Mace, G.M.; Lande, R. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology*. 5: 138–157.
- McCarthy, M.A.; Burgman, M.A.; Ferson, S. 1996. Logistic sensitivity and bounds for extinction risks. *Ecological Modelling*. 86: 297–303.
- McCarthy, M.A.; Lindenmayer, D.B. 1999. Incorporating metapopulation dynamics of greater gliders into reserve design in disturbed landscapes. *Ecology*. 80: 651–667.
- Menges, E.S. 1990. Population viability analysis for an endangered plant. *Conservation Biology*. 4: 52–62.
- Millar, C.I.; Ledig, F.T.; Riggs, L.A. 1990. Conservation of diversity in forest ecosystems. *Forest Ecology and Management*. 35: 1–5.
- Miller, R.S.; Botkin, D.B. 1974. Endangered species models and predictions. *American Scientist*. 62: 172–181.
- Mills, L.S.; Doak, D.F.; Wisdom, M.J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*. 13: 815–829.
- Morris, W.; Doak, D.; Groom, M. [and others]. 1999. A practical handbook for population viability analysis. *The Nature Conservancy*. 80 p.
- Newbold, C.D. 1996. The effects of tornado and clearcut disturbances on breeding birds in a Tennessee oak-hickory (*Quercus-Carya* spp.) forest. Knoxville, TN: University of Tennessee. 116 p. M.S. thesis.
- Noon, B.R.; McKelvey, K.S. 1996. Management of the spotted owl: a case history in conservation biology. *Annual Review of Ecology and Systematics*. 27: 135–162.
- Noss, R.F.; Cooperrider, A.Y. 1994. *Saving nature's legacy: protecting and restoring biodiversity*. Covelo, CA: Island Press. 416 p.
- Nunney, L.; Campbell, K.A. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution*. 8: 234–239.
- Pfab, M.F.; Witkowski, E.T.F. 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R.A. Dyer under four management scenarios. *Biological Conservation*. 96: 263–270.
- Pimm, S.L.; Gilpin, M.E. 1989. Theoretical issues in conservation biology. In: Roughgarden, J.; May, R.M.; Levin, S.A., eds. *Perspectives in ecological theory*. Princeton, NJ: Princeton University Press: 287–305.
- Pimm, S.L.; Jones, H.L.; Diamond, J.M. 1988. On the risk of extinction. *American Naturalist*. 132: 757–785.
- Possingham, H.P.; Davies, I. 1995. ALEX: a model for the viability analysis of spatially structured populations. *Biological Conservation*. 73: 143–150.
- Probst, J.R.; Crow, T.R. 1991. Integrating biological diversity and resource management. *Journal of Forestry*. 89: 12–17.
- Roloff, G.J.; Haufler, J.B. 1997. Establishing population viability planning objectives based on habitat potentials. *Wildlife Society Bulletin*. 25: 895–904.
- Ruckelshaus, M.H.; Hartway, C.; Kareiva, P.M. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology*. 11: 1298–1306.
- SAS Institute Inc. 1990. *SAS/STAT user's guide*. Version 6. 4th ed. Cary, NC: SAS Institute Inc. 705 p.
- Schroeder, R.L. 1983. Habitat suitability index models: pileated woodpecker. FWS/OBS–82/10.39. [Washington, DC]: U.S. Department of the Interior, Fish and Wildlife Service. 15 p.
- Schulte, L.A.; Niemi, G.J. 1998. Bird communities of early-succession burned and logged area. *Journal of Wildlife Management*. 62: 1418–1429.
- Shaffer, M.L. 1981. Minimum viable population sizes for species conservation. *BioScience*. 31: 131–134.
- Shaffer, M.L. 1983. Determining minimum viable population sizes for the grizzly bear. *International Conference on Bear Research and Management*. 5: 133–139.
- Shaffer, M.L.; Samson, F.B. 1985. Population size and extinction: a note on determining critical population size. *American Naturalist*. 125: 144–152.
- Smith, D.M.; Larson, B.C.; Kelty, M.J.; Ashton, P.M.S. 1996. *The practice of silviculture: applied forest ecology*. New York: John Wiley. 537 p.
- Soulé, M.E., ed. 1987. *Viable populations for conservation*. New York: Cambridge University Press. 189 p.
- Stacey, P.B.; Taper, M. 1992. Environmental variation and the persistence of small populations. *Ecological Applications*. 2: 18–29.
- Taylor, B.L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology*. 9: 551–558.
- Temple, S.A. 1986. The problem of avian extinctions. *Current Ornithology*. 3: 453–485.

- Thomas, C.D. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conservation Biology*. 4: 324–327.
- Thompson, F.R., III. 1993. Simulated responses of a forest interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology*. 7: 325–333.
- Thompson, F.R., III; Dijak, W.; Kulowiec, T.; Hamilton, D. 1992. Breeding bird populations in Missouri Ozark Forest with and without clearcutting. *Journal of Wildlife Management*. 56: 23–30.
- U.S. Department of Agriculture, Forest Service. 1997. FY 1996 forest management program annual report–national summary. Publ. FS-614. Washington, DC. 117 p.
- White, D.; Minotti, P.G.; Barezak, M.J. [and others]. 1997. Assessing risks to biodiversity from future landscape change. *Conservation Biology*. 11: 349–360.
- White, G.C. 2000. Population viability analysis: data requirements and essential analyses. In: Biotani, L.; Fuller, T.K., eds. *Research techniques in animal ecology*. New York: Columbia University Press: 288–331.
- Wilcox, B.A.; Murphy, D.D. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist*. 125: 879–887.
- Young, A.C.; Clarke, G.M., eds. 2000. *Genetics, demography and viability of fragmented populations*. Cambridge, United Kingdom: Cambridge University Press. 438 p.