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DYNAMIC HABITAT AND POPULATION ANALYSIS: AN APPROACH TO RESOLVE THE BIODIVERSITY MANAGER'S DILEMMA

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Abstract. Biodiversity managers face a dilemma of choosing between "coarse-filter" approaches that deal with the habitats of several species and "fine-filter" approaches that address population viability of one or a few species. We present an approach for local spatial scales that integrates habitat-based and population-based methods to focus research and management on the species in a community that are most at risk of extinction and on the places in the landscape most important to these species. The steps in Dynamic Habitat and Population (DHP) Analysis are:

1) determine which species in the planning area most merit field study based on existing data;
2) use local field data to select species that most merit demographic study;
3) use demographic data to model population viability of the species deemed most at risk;
4) design and evaluate alternative management strategies for key species and landscape settings.

We review each step and provide an example for land birds in a portion of the Greater Yellowstone Ecosystem. Among the 143 species of land birds likely in the study area, we selected 13 species most at risk of extinction. These were mostly neotropical migrant passerines that specialized on low-elevation deciduous habitats that may serve as population source areas. We present a management plan for the multiple ownerships of the study area that seeks to maintain/restore population source habitats for key species.

DHP Analysis provides a framework for biodiversity management for those regions identified as high priority for conservation by continental-scale assessment programs such as Gap Analysis. Our approach is designed to minimize local extinctions, which should reduce the risk of range-wide extinctions.

Key words: biodiversity; conservation; Gap Analysis; Greater Yellowstone Ecosystem; management; population viability; risk assessment; species prioritization.

INTRODUCTION

It is widely appreciated that managers of biodiversity must prioritize conservation efforts so that the ecosystems and species most at risk of extinction are given appropriate attention (Scott et al. 1987, Milsap et al. 1990, Avery 1994, Allendorf et al. 1997). Several approaches have been applied at various spatial scales to rank the vulnerability of ecosystems and species, and to more intensively manage those most at risk (Table 1). Generally applied at the physiographic province to continental scales, Gap Analysis (Scott et al. 1993, Scott et al. 1996) and Critical Ecosystems Analysis (Noss and Cooperrider 1994) are used to identify the ecosystems supporting numerous and/or unique species that are poorly protected. Similarly, Species Prioritization schemes (Masters 1991, Milsap 1995) identify the species within a province to continental area that are likely at high risk of extinction. For watershed scales, Ecological Process Management (e.g., Boyce 1991, Cissel et al. 1994) seeks to maintain key ecological processes like disturbance and succession in order to maintain species adapted to these processes. Dynamic Habitat Modeling (Hansen et al. 1993, White et al. 1997) assumes that species abundances are related to habitat suitability and simulates change in habitats across watersheds under alternative management scenarios. Finally, Population Viability Analysis conducts demographic analyses of single species to assess likelihood of extinction.

Most of these approaches are so-called "coarse-filter" (Nature Conservancy 1982, Hunter 1990, Noss and Cooperrider 1994) in that they manage key ecosystems or habitats in hopes of maintaining the species within them. Population Viability Analysis (PVA), in contrast, is termed a "fine-filter" approach because it focuses on demography of individual species.

Choosing between coarse- and fine-filter approaches might be termed the "biodiversity manager's dilemma." Most managers seek to maintain viable populations of native species in order to avoid local and range-wide extinctions. In the United States, the National Forest Management Act of 1976 directs the maintenance of viable populations of native vertebrates that are well distributed across their ranges. Managers could

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TABLE 1. Current approaches for prioritizing and managing ecosystems and species at various spatial scales and the new method presented in this paper (the new method is in bold type).

Name	Scale	Concept	Method	Examples
Gap Analysis/Critical Ecosystems	Province to continental	Identify ecosystems that contain species and/or processes that are poorly protected so that local management can be applied.	Rank ecosystems based on native species, threats to ecosystem, and other factors.	Nature Conservancy (1982), Scott et al. (1993), Noss and Cooperrider (1994)
Species Prioritization	Province to continental	Identify species most at risk so that management can be directed at them.	Use existing life history and other data to rank species viability.	Millsap et al. (1991), Hunter et al. (1993)
Ecological Process Management	Watershed to province	Maintain key ecological processes and landscape structures to maintain species adapted to these conditions.	Analyze interactions among ecological processes and structures and manage to maintain them.	Boyce (1991), Cissel et al. (1994)
Dynamic Habitat Modeling	Watershed to province	Use configuration of suitable habitat for each species as a measure of extinction risk.	Quantify/project change in suitable habitats for each species under varying management scenarios.	Hansen et al. (1993), (1995), White et al. (1997)
Dynamic Habitat and Population Analysis	**Watershed to province**	**Identify the species and places most at risk and focus research and management on these.**	**Use a hierarchical set of filters to identify and manage the species and places most at risk.**	**This paper**
Population Viability Analysis	Watershed to range	Analyze population demography to assess risk of extinction.	Use complex demographic models to assess species viability under varying management strategies.	Shaffer (1981), Murphy and Noon (1992)

best comply with this law using fine-filter approaches. However, the demographic data needed are often difficult and expensive to obtain. Estimating population vital rates and densities usually requires extensive field study. Moreover, these rates vary spatially in many ecosystems, necessitating knowledge about dispersal and spatially explicit field study and population modeling (Dunning et al. 1995). Such intensive single-species studies can cost hundreds of thousands to millions of dollars per year (Mann and Plummer 1992). Because of these costs, Population Viability Analysis is often done only for economically valuable species (e.g., game species) or endangered species, while the demographies of the myriad of other species in a planning area are ignored.

The alternative coarse-filter approach assumes that the population status of species is correlated with habitat availability. In this case, the area and spatial patterning of ecosystems or habitat types are quantified and rule-based or statistical functions are applied that predict the presence or abundance of a species as a function of the habitat. While the coarse-filter approach is attractive in being less costly and allowing many species in a community to be considered, it has serious limitations (Hansen et al. 1993, Scott et al. 1993, Conroy and Noon 1996). The accuracy of the habitat models in predicting species presence or abundance is seldom quantified, and is likely to be variable and often low if local field data are not used. Also, the abundance of a species in a habitat may not be indicative of rates of survival and reproduction in that habitat (van Horne 1983). For example, a species may be abundant in a habitat where reproduction does not replace mortality if there is immigration into the habitat from other population source habitats (Pulliam 1988, Pulliam and Danielson 1991). Such source/sink dynamics are probably common in landscapes where resources and conditions ere relatively heterogeneous in space (Pulliam 1996; Hansen and Rotella 1999). Under the coarse-filter approach, then, species could undergo population declines or even extinction without the knowledge of biodiversity managers.

The biodiversity manager's dilemma is especially expressed at local to regional spatial scales. Detailed demographic studies over entire species ranges are not feasible for more than a few species; hence the coarse-filter approaches are logical at continental scales. Gap Analysis is being applied across the United States, for example, to identify regions rich in native species that are currently poorly protected. What remains unresolved is what combination of coarse- and fine-filter conservation approaches should be applied at local scales to best complement Gap Analysis and other continental-scale coarse-filter approaches. In practice, many managers do not face a dilemma in choosing between biodiversity strategies because funding limits them to coarse-filter approaches. However, an increasing number of studies are finding that spatially medi-

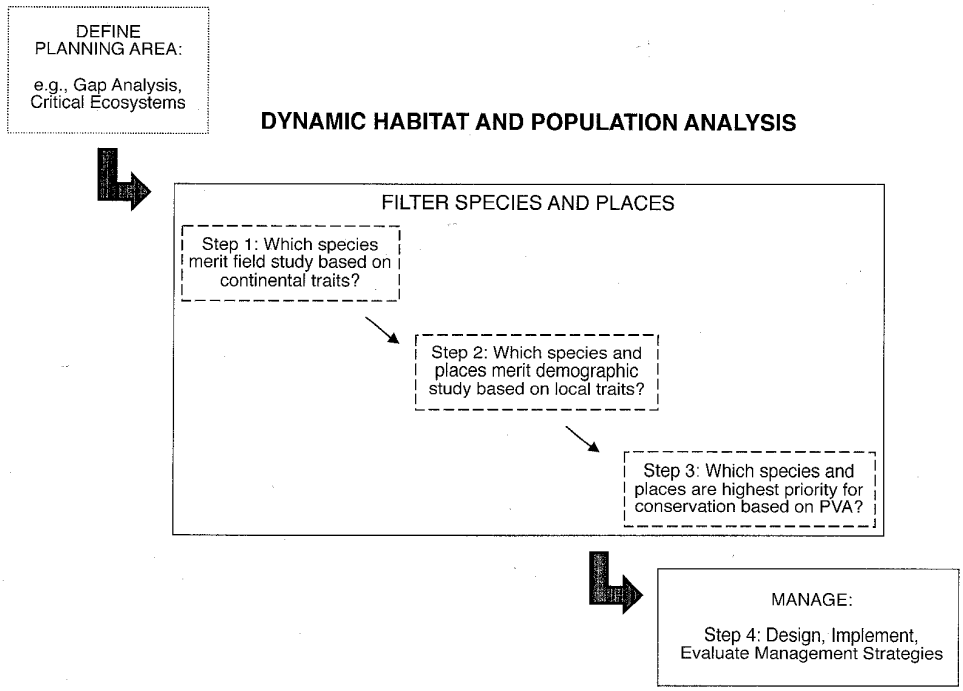

FIG. 1. A conceptual model depicting DHP Analysis. Once a planning area is defined based on Gap Analysis, Critical Ecosystems Analysis, or administrative boundaries, species and places in the planning area are analyzed with a series of screens to determine which are highest priorities for conservation. Appropriate management plans are then crafted and evaluated.

ated population dynamics are prevalent in nature and strongly influence population viability (Pulliam 1996). It is likely that the pressure to integrate fine-filter approaches in biodiversity management will increase in the future, heightening the dilemma.

We propose an approach to help resolve the biodiversity manager's dilemma at local spatial scales (small watershed to regional). Our Dynamic Habitat and Population (DHP) Analysis integrates aspects of Species Prioritization, Dynamic Habitat Modeling, and PVA into a cost-effective management framework. It is designed to bridge coarse-filter studies of habitats with species-specific studies of population demography and viability at local spatial scales. In this paper, we describe the steps in DHP Analysis and illustrate each in an example from the Greater Yellowstone Ecosystem.

General Approach

The basic assumption of the approach is that a subset of the species and places in a locality have the greatest viability risk. A filtering approach is used to focus increasingly detailed study and management strategies on these places and species. As these screens are increasingly expensive to conduct, the result is that available resources are directed toward the species and places that are of the greatest concern. Management strategies to maintain these key species and places in the landscape can then be crafted and implemented.

Once a planning area is defined based on Gap Analysis or other factors, the steps of DHP Analysis (Fig. 1) are applied as follows.

1) Determine which of the species in the planning area most merit field study by ranking each species' viability risk based on range-wide population status, habitat use, and threats to habitat.

2) Screen these selected species based on field study and analyses of local habitat and population factors and range-wide vulnerability scores to determine which most merit field study of local demography.

3) Obtain and use local data on reproduction, survival, and/or dispersal in key places in the landscape to parameterize population models and assess population viability of the subset of species deemed most at risk.

4) Design and evaluate alternative management strategies for the species identified as most at risk and the landscape settings most important to these species.

This approach is designed to be hierarchical, so that the latter steps do not necessarily need to be completed to initiate management designs. Financial resources and time may dictate how many of Steps 1–3 are completed before moving to management design in Step 4.

Step 1: Screening Based on Range-wide Variables

A local population has enhanced conservation importance if the species has high threat of extinction

across its range. Hence, our first screening involves range-wide measures of population status, habitat use, and threats to habitats. This step is consistent with the several species prioritization studies that have been published (Masters 1991, Millsap et al. 1991, Hansen et al. 1993, Hunter et al. 1993, Avery et al. 1994, Mace 1994, Mace and Collar 1994, Reed 1995, Carroll et al. 1996, Hedenas 1996, Lunney et al. 1996, Freitag et al. 1997). Though not yet recognized in conservation biology texts, these prioritization schemes have been widely used to identify the species that merit more intense conservation and management.

The conceptual foundation of Species Prioritization recognizes that not all species are equally prone to extinction. Species that have suffered local extinction often share certain demographic and life history traits (Whitcom et al. 1981, Pimm et al. 1988, Laurance 1991). Species with small population sizes are often at risk due to vagaries in birth and death rates, environmental fluctuation, and random genetic processes (Shaffer 1981). Even moderate to large populations, however, may be prone to extinction if they are sensitive to habitat change by being narrowly distributed, require two or more habitats, or are disrupted by habitat fragmentation (Pimm et al. 1988). Similarly, species with low reproductive rates may be slow to rebuild following population crashes (Pimm et al. 1988), and those aggregated in one population cannot enjoy the benefits of being "rescued" by emigrants from other subpopulations (Brown and Kodric-Brown 1977). As humans increasingly dominate the biosphere (Vitousek et al. 1997), species that are especially sought by humans or require the habitats that humans preferentially occupy are also extinction prone (Hunter 1996). The Species Prioritization studies cited above have used several ecological, life history, and phylogenetic variables to rank extinction proneness, and applied them at watershed, regional, and continental scales.

Rigorous tests of the accuracy of these approaches are relatively few. Millsap et al. (1990), working with vertebrates in Florida, found that recently extinct species had among the highest vulnerability scores and that species unlisted by state and federal agencies had lower mean scores than species listed as of special concern, threatened, or endangered. Hansen and Urban (1992) found that the vulnerability scores of birds to habitat fragmentation were significantly correlated with independent data on population trends. The most rigorous test to date was by Parent and Schriml (1995), who developed a logistic function to predict extinction risk based on life history attributes for fish in the Great Lakes–St. Lawrence biozone. The function was then applied to fish species in the American Midwest, and successfully classified species previously identified as at risk with a 78% accuracy.

Efforts to prioritize species have often used similar methods. A list of the species for the area of interest is derived from range maps, national or provincial checklists, or occurrence maps (e.g., Nature Conservancy 1982). Traits thought to relate to extinction proneness are then compiled for each species. While there has been considerable overlap in the variables used in the studies cited above, each author selected variables and spatial scales consistent with their objectives and location. A typical constraint on selection of variables is the quality of available data. Detailed and accurate data are often available for a small subset of the species in an area. Thus, more general and qualitative data are often used to allow most species in the area to be considered. Potential data sources in order of increasing resolution and accuracy are: field guides (e.g., Burt and Grossenheider 1976), taxon-specific handbooks (e.g., Ehrlich et al. 1988), encyclopedic accounts of taxa (Bent 1953), quantitative local or national survey data (e.g., Tucker et al. 1994), and published scientific studies.

Methods for scoring sensitivity to extinction vary from nominal, to ordinal, to interval (i.e., Zar 1974), depending on the nature of data available. Combining the scores for several variables into one index of sensitivity to extinction was often done by summing the scores of the individual variables or weighting some variables more heavily than others. Reed (1995) recommended multivariate statistical approaches as being more objective and informative than simply combining scores across traits. Knowledge of the species and type and quality of the data available are often the deciding factors on the approach used. For example, without knowledge of which of the candidate traits may be most important in determining vulnerability to extinction, conservationists have generally given equal weight to all of the traits that may put a species at risk.

The final challenge in rating species is to establish cut-offs to identify the set of species of highest conservation priority. As the species in a community typically represent a gradient in vulnerability to extinction, any cut-off level is necessarily subjective. Some authors have used the mean or range of scores for federally listed species as a guide to establishing scoring cut-offs (Millsap et al. 1990). Others have simply designated the 20% or so of species with the highest sensitivity scores as those most meriting special consideration. Multivariate clustering techniques can be used to establish cut-offs based on within-group vs. between-group variance (Given and Norton 1993, Hall 1993, Reed 1995).

Greater Yellowstone Ecosystem example

We demonstrate DHP Analysis in the Greater Yellowstone Ecosystem (GYE) as a guide to readers who may wish to apply the method elsewhere. The GYE was selected because of our ongoing research there and because the mixed management jurisdictions and human population growth there offer challenges to maintaining native species. We deal only with land birds because they are the main focus of our research. The

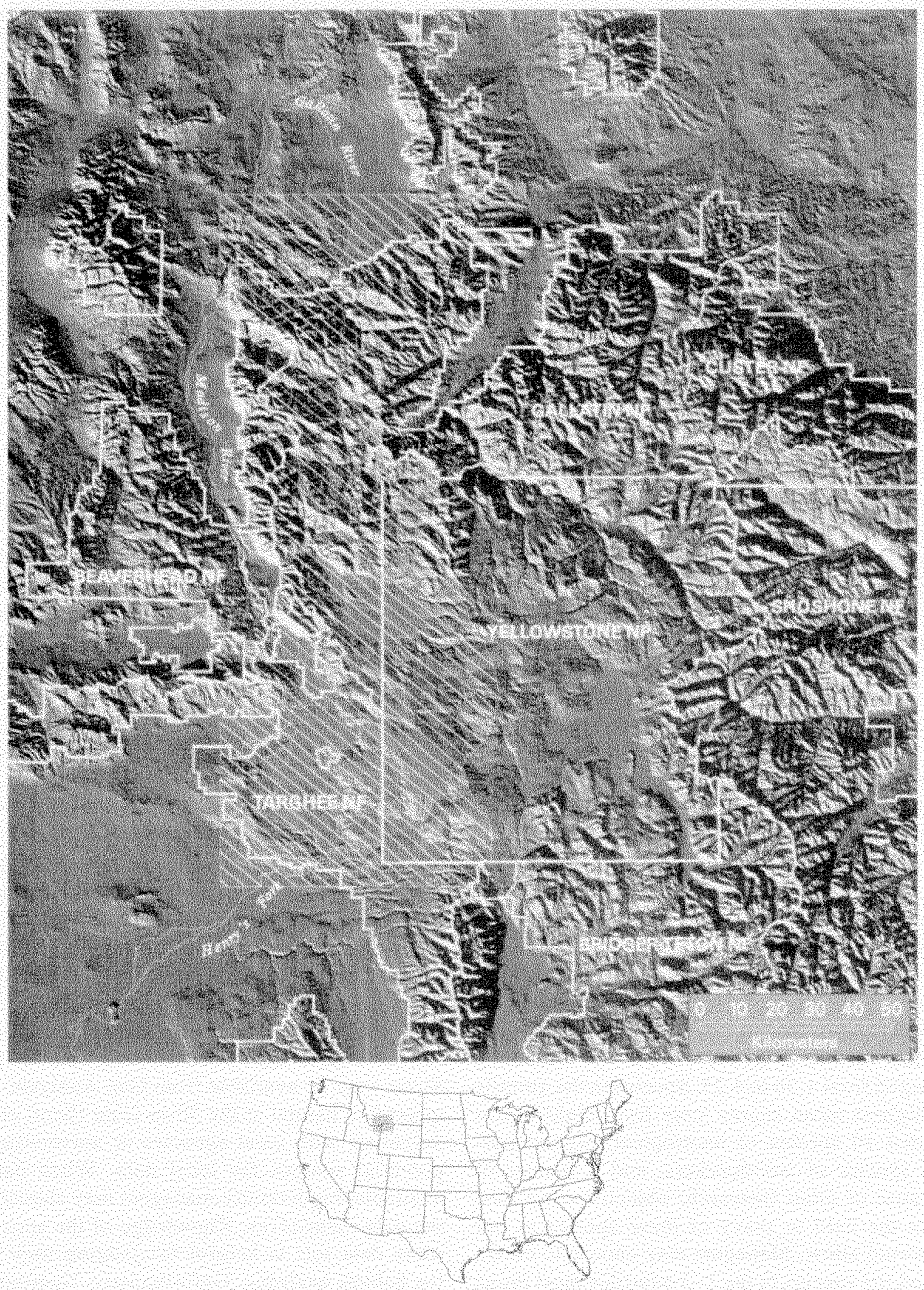

FIG. 2. Shaded relief map of the Greater Yellowstone Ecosystem and the study area (hatched), which includes the upper portions of the Gallatin, Madison, and Henry's Fork watersheds.

bird data are based on the results from the first two years of a 5-yr study of factors controlling bird diversity and demography. As is the case for many places, current knowledge of species and processes in the GYE is insufficient to rigorously apply all the steps of DHP Analysis. A strength of the approach, however, is that it applies best current knowledge to management. In this regard, the management plan derived for our planning area can be improved as new knowledge accumulates.

Our planning area includes the upper Gallatin, Madison, and Henry's Fork watersheds in Montana, Idaho, and Wyoming, USA (Fig. 2). These rivers originate on a plateau in Yellowstone National Park (YNP) and flow through adjacent national forests to privately owned agricultural floodplains in the lowlands. Strong topo-

graphic gradients cause relatively favorable climate and soil fertility only at lower elevations (Despain 1990, Rodman et al. 1996). Lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and sage (*Artemesia* spp.) habitats dominate higher elevations (Despain 1990). Douglas-fir (*Pseudotsuga menziesii*) occurs on richer soils at mid-elevations. Deciduous communities of willow (*Salix* spp.), aspen (*Populus tremuloides*), and cottonwood (*Populus* spp.) grow where soil moisture is high on toeslopes and in valley bottoms. Wildfire has been common in YNP, while timber harvest has been moderate to heavy in the Targhee and Gallatin National forests. The towns and small cities in the valley bottoms are surrounded by agricultural and rural residential land uses.

For the first step, we compiled a list of land bird species known to breed within quarter latitude/longitude cells overlapping the study area (Stephens and Sturts 1991, Ellis et al. 1996, Luce et al. 1997). Criteria for this screening were derived from the scheme of the Partners in Flight Program (PIF) (Hunter et al. 1993) (Table 2). We selected the PIF scheme because the criteria largely reflect the traits of extinction-prone species, some of the variables are based on the Breeding Bird Survey (BBS) data (Robbins et al. 1986), and the scoring has been done for nearly all bird species in our planning area by regional and national experts. We elected to weight the variable population trend more heavily (it was multiplied by 1.5) because we felt that it is especially relevant to likelihood of extinction (see Avery et al. 1994:137). A mean was then derived for the seven screening variables.

Land birds known to breed in the vicinity of the planning area include 143 species. BBS data were not available for seven of these species, and they were not ranked by the PIF Program. As each of these species is on the periphery of its range here, we did not consider these species further. Mean scores for the remaining species ranged from 1.36 to 4.25. Species in the quintile with the highest mean scores were from eight orders and included 10 species of neotropical migrant passerines, 3 species of woodpeckers, and 2 species of owls. Because of other (research) objectives, we then sampled in the field as many of these species as our methods would allow. Managers may choose to obtain field data on the species in the 1–3 quartiles most prone to extinction, as their resources permit.

Step 2: Screening Based on Local Habitat Variables

Ecologists have long found associations between the distributions of habitats and the abundances of species. Hence, we commonly predict organism abundance based on habitat characteristics. The theoretical basis of this is found in the ideal free distribution model of Fretwell and Lucas (1970), which asserts that individuals within a population will distribute themselves among habitats so as to maximize individual fitness. When habitats are saturated, population density within a habitat will be proportional to habitat quality. While recent work on spatially mediated population dynamics has revealed several important alternatives to the ideal free distribution model (see Step 3 below), it remains clear that habitat attributes set an upper limit on population abundance and fitness. Hence, we can use analyses of habitat to identify species that are likely to have small populations in a planning area.

Species habitat associations often vary among ecosystems and sometimes vary over time. Thus, local studies of habitat use are often needed for accurate prediction of species abundance. Key steps are to determine the habitat requirements of species, map the distributions of these habitat factors over the planning area, extrapolate species abundance across the planning area based on habitat associations, and analyze the predicted patterns of species distributions. Habitat is often quantified in terms of vegetation structure and composition at the stand and landscape levels. The predictive ability of species habitat models can sometimes be improved by also considering abiotic factors such as climate, topography, soil, and water regime (Hansen and Rotella 1999). Such abiotic factors may directly limit the abundance or demography of a population or indirectly influence organisms by altering disturbance regimes and vegetation structure or by altering energy flow. See Table 1 in Hansen and Rotella (1999) for a list of the types of variables that may be useful predictors of organism abundance and species richness.

Such habitat data are increasingly available around the world, although their temporal and spatial resolution vary substantially from place to place. Data of continental extent can often be found on the World-Wide Web. Such data for climate and vegetation sometimes have a minimum resolution of 1 km^2, which may be appropriate for regional-scale studies, but too coarse for more local studies. Finer scale data for the United States may be available from Gap Analysis, which has quantified habitat at the 30-m scale (Scott et al. 1993). Scientists with local agencies or universities are also potential sources for local data. When data are not available, biodiversity managers may choose to collect the data themselves. Knowledge of the accuracy of all these data sets is helpful for judging their suitability for habitat analyses. Unfortunately, rigorous accuracy assessments are seldom available for data obtained from other sources.

Estimating species abundances by habitat type from field studies remains labor intensive. However, relatively cost-effective methods that sample several species simultaneously are increasingly available. Examples of these are quadrat sampling for plants, sticky traps and sweep netting for invertebrates, pitfall traps for herptiles, live traps for small mammals, and point counts for birds (Sutherland 1996). Carefully designed sampling schemes can help to make such studies as efficient and cost-effective as possible. For example, it

is often desirable to stratify the sample locations by the environmental variables that are most likely to be related to species abundances. Randomizing relative to other predictor variables allows for exploratory analyses of the influence of these variables on the organisms of interest. Decisions about sample sizes, season of sampling, and temporal duration of sampling must be made based on knowledge of the ecology of the organisms, ecosystem variability, and resources available for sampling.

Several statistical methods are available for determining the strengths of association among predictor variables and species abundance and for extrapolating species abundance over the planning area (e.g., Capen 1981, Verner et al. 1986, Morrison et al. 1992, Mauer 1994). It is helpful to hold back some of the field data from the initial analysis to assess the accuracy of the predictions of the resulting models.

Greater Yellowstone Ecosystem example

Elevation was derived from digital elevation models for the planning area. We additionally classified vegetation cover type and seral stage from Landsat Thematic Mapper imagery from 1991. Bird abundance was sampled within 100 stands that were stratified by cover type, seral stage, and elevation. The fixed-radius plot method (Ralph et al. 1993) was used to estimate bird abundance at six census points distributed 200 m apart in each sample stand. Either two or three censuses were done during the bird breeding seasons of 1995–1996. This method does not adequately sample raptorial birds and these were omitted from the analysis.

The vegetation mapping revealed that mature lodgepole pine was the dominant cover type, covering 45% of the planning area. For other cover types, areas were: sapling-aged lodgepole pine (23%), Douglas-fir (14%), grasslands (9%), and sage shrublands (5%). Deciduous habitats, willow (2%), aspen (1%), and cottonwood (1%), were associated with riparian zones or groundwater seeps at lower elevations.

A total of 113 species were sampled in the field in 1995 and 1996, 61 of which were in quintiles 3–5 in the Step 1 screening. We elected to include all 117 species in Step 2 screening because local data were in hand for them. Multiple regression analyses revealed that cover type and seral stage explained 60% of the variation in species richness in 1995 and 1996. These variables were significantly related to the abundances of most individual bird species. Several species were uniquely associated with cottonwood, aspen, or willow habitats. A smaller number of species specialized either on grassland, sage-shrub, or conifer cover types. Bird species richness was negatively related to elevation in 1995, but no significant relationship was detected in 1996. Cover type and seral stage were used as the basis for predicting bird abundance by habitat type for Screening 2.

We used four local scale and two broader scale variables in the Step 2 screening. The local variables included total population size, habitat abundance, nest predation risk, and nest parasitism risk. The two nonlocal-scale variables were reproductive effort and the mean of the sensitivity score from the first screening. Reproductive effort is relevant because it is a measure of the ability of a population to rebound after a population decline. Methods used to derive each variable are described in Table 2.

An index of risk of extinction was generated for each species by first assigning scores for each variable on a scale of 1 (least at risk) to 5 (most at risk). This was done by ordering the species list by the value of a variable and assigning each species to a quintile based on the ordinal ranking (Appendix A). A mean score for the quintiles of the six variables was then calculated for each species. Species in the quintile with the highest mean scores were considered the most at risk and most meriting conservation attention. We also summarized the traits of species at high and low risk of extinction using principal components analysis (PCA) on the original predictor variable values (not the quintiles).

We found that the first two principal components accounted for 57% of the variation in the data set. PC I distinguished species based on population size, habitat area, reproductive effort, and susceptibility to predators and parasites (Fig. 3). PC II separated species based on extinction scores from Screen 1. Species that ranked in the Step 2 screen as most vulnerable to extinction (quintile 5) were located in the lower right-hand quadrat of the PCA space. They tended to have small populations and habitats, low reproductive efforts, high susceptibility to nest predators and parasites and were ranked as highly vulnerable to extinction in Screen 1. Most of these nested in the deciduous habitats, including American Redstart (*Setophaga ruticilla*), Willow Flycatcher (*Empidonax traillii*), Veery (*Catharus fuscescens*), Western Wood-Pewee (*Contopus sordidulus*), Orange-crowned Warbler (*Vermivora celata*), Northern Oriole (*Icterus galbula*), Least Flycatcher (*Empidonax minimus*), and Cedar Waxwing (*Bombycilla cedrorum*) (Appendix B). Two cavity nesters, the Violet-green Swallow (*Tachycineta thalassina*) and the Red-naped Sapsucker (*Sphyrapicus nuchalis*), scored in this quintile because of their specialization on aspen and/or cottonwood habitats and low abundances. The one species in this group associated with conifer habitat, Hammond's Flycatcher (*Empidonax hammondii*), was highly susceptible to predation, had a low reproductive effort, and was scored as highly at risk in Screen 1. Also in this quintile were the Spotted Towhee (*Pipilo erythrophthalmus*), a shrub associate, and the Bobolink (*Dolichonyx oryzivorus*), a grassland species.

Some members of this group had very low abundances in the study area for reasons that cause little concern for management. The study area is at the edge of the ranges of Red-eyed Vireo (*Vireo olivaceus*),

TABLE 2. Criteria used to screen vulnerability to extinction in this study. Criteria for Screening Level 1 are from Hunter et al. (1993).

Screening level	Variable	Spatial scale	Definition	Score
1	Relative abundance	Species range	Mean number of birds per Breeding Bird Survey route for the 10 highest routes in the species range averaged over the years 1985–1991.	1) Abundant (≥100) 2) Common (30–99) 3) Uncommon to fairly common (10–29) 4) Rare to uncommon (1–9) 5) Very rare to rare (<1)
1	Breeding distribution	Species range	Breeding range covers this percentage of temperate North America or equivalent area.	1) Very widespread (≥76–100%) 2) Widespread (51–75%) 3) Intermediate (26–50%) 4) Local (11–25%) 5) Very local (≤10%)
1	Winter distribution	Species range	Categories grade from: (1) southern United States to South America; to (5) local Latin American regions.	1) Very widespread 2) Widespread 3) Intermediate 4) Local 5) Very local
1	Threats in nonbreeding range	Species range	Uncertainty in threats to breeding and nonbreeding ranges may also be considered.	1–5 based on the percentage of habitat that has not changed since 1945 and anticipated changes in habitat in coming decades.
1	Threats in breeding range	Physiographic region	As above	As above
1	Importance of area (in relative abundance)	Physiographic region	Percentages of abundance in the physiographic region of interest to the maximum species abundance for all physiographic regions.	1) Accidental 2) 0–5.9% 3) 6–24.9% 4) 25–49.9% 5) 50–100%
1	Population trends	Physiographic region	Based on percentage change in population size as measured in BBS data and based on knowledge uncertainty.	1) Large increase 2) Increase 3) Trend unknown or stable 4) Decrease 5) Large decrease
2	Local relative abundance	Planning area	Based on ranking of estimated absolute abundance among species. Absolute abundance is the sum of the average density of a species in each habitat times the area of that habitat.	Ranked from 1 (most abundant) to 5 (least abundant) based on ordinal quintile.
2	Habitat area	Planning area	Percentage of the study area occupied by habitats where the species has an average density that is ≥50% of the maximum average density in a habitat.	Ranked from 1 (largest area) to 5 (smallest area) based on ordinal quintile.
2	Predator/prey ratio†	Planning area	Average ratio of avian nest predators to the prey species across all habitats that contain ≥10% of the total prey population.‡	Ranked from 1 (highest) to 5 (lowest) based on ordinal quintile.
2	Brood-parasite/host ratio§	Planning area	Average ratio of Brown-headed Cowbirds to the host species across all habitats that contain ≥10% of the total host population.	Ranked from 1 (most abundant) to 5 (least abundant) based on ordinal quintile.
2	Reproductive effort	Breeding range	Average clutch size times the average number of clutches per breeding season.	Ranked from 1 (largest) to 5 (smallest) based on ordinal quintile.

TABLE 2. Continued.

Screening level	Variable	Spatial scale	Definition	Score
2	Screening 1 mean score	Physiographic region	Mean value among the seven variables used in Screening 1.	Ranked from 1 (largest) to 5 (smallest) based on ordinal quintile.
3	Nest success	Planning area	Number of young fledged per nesting attempt.	Ranked from 1 (largest) to 5 (smallest) based on ordinal quintile.
3	Survival rate	Planning area	Not used in this study.	

† The ratio was multiplied by 1 if the species has a nest type that is susceptible to avian predators and by 0 if the nest type precluded avian nest predation.

‡ Included in the predator guild were American Crow, Black-billed Magpie, Clark's Nutcracker, Common Raven, Gray Jay, and Steller's Jay.

§ The ratio was multiplied by 1 for hosts that are commonly parasitized by cowbirds and do not have strong defensive mechanisms and by 0 for species that are either not selected by cowbirds or have evolved effective defensive behaviors (following Ehrlich et al. [1998]).

Common Grackle (*Quiscalus quiscula*), and Gray Catbird (*Dumetella carolinensis*). The Red-winged Blackbird (*Agelaius phoeniceus*) and American Goldfinch (*Carduelis tristis*) were rare because their preferred habitats are not found here. Finally, the Eastern Kingbird (*Tyrannus tyrannus*)was not adequately sampled by our methods.

Species scored as least vulnerable to local extinction in the Step 2 screen were mostly located in the upper left-hand quadrat of the PCA space and had traits opposite those in quintile 5. Examples are Mountain Chickadee (*Parus gambeli*) (common in coniferous forests and nests in cavities), American Robin (*Turdus migratorius*) (abundant habitat generalist), and the

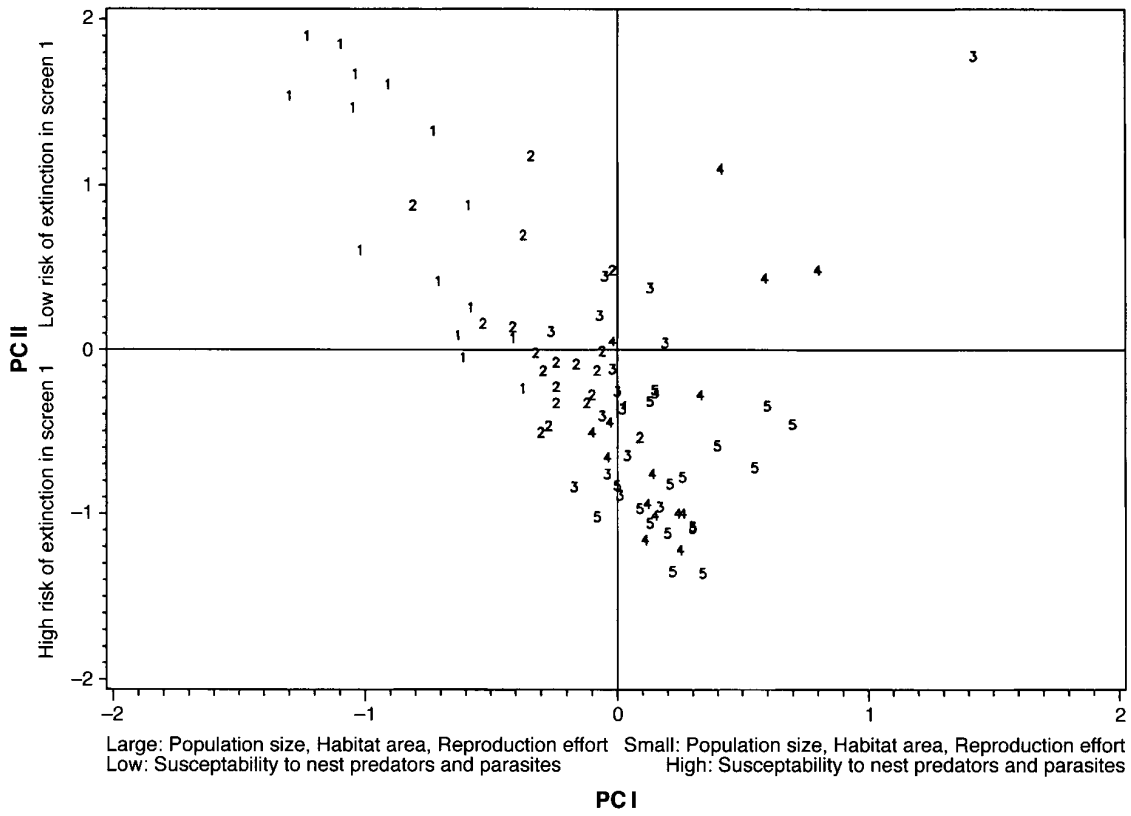

FIG. 3. Locations of bird species along principal components axes 1 and 2 of an analysis of the traits of bird species included in viability Screening 2. Species are denoted by their Screening 2 risk of extinction scores.

Brown-headed Cowbird (*Molothrus ater*) (brood parasite).

Species in quintiles 3 and 4 that appear to be of management concern include deciduous specialists (Northern Waterthrush, *Seiurus noveboracensis*; Dusky Flycatcher, *Empidonax oberholseri*; Ruffed Grouse, *Bonasa umbellus*; Common Yellowthroat, *Geothlypis trichas*), conifer specialists (Olive-sided Flycatcher, *Contopus borealis*; Steller's Jay, *Cyanocitta stelleri*), a sage-shrubland associate (Brewer's Sparrow, *Spizella breweri*), and several generalists (Blue Grouse, *Dendragapus obscurus*; MacGillivray's Warbler, *Oporornis tolmiei*; and Wilson's Warbler *Wilsonia pusilla*). The very low abundances of Black-backed Woodpecker (*Picoides arcticus*) (recent fire associate) suggest that they are also vulnerable.

These results led us to select for more intense demographic field study those species in quintiles 3–5 described above as most at risk. Because aspen, cottonwood, and willow habitats are very small in area, appear to be declining in area over time, support many of the species most at risk, and support high bird species richness, these habitats represent places in the landscape of particular conservation concern.

Step 3: Screening Based on Local Demography

As mentioned above, the abundance of a local population may not be a good measure of its extinction risk. Thus demographic analyses should be done for species deemed most at risk in the Step 2 screening and in the habitats most important for these species. Demographic analyses consider a population's birth, death, and dispersal rates and can be used to assess the population's risk of extinction. Risk assessment, or Population Viability Analysis (PVA), calculates the likelihood that the population will fall below a given size (Ginzburg et al. 1982, Burgman et al. 1993). Several approaches are available for performing PVAs (see Starfield and Blelock 1986, Renshaw 1991, Burgman et al. 1993) and predictions can vary according to the approach (Boyce 1992, 1997, Mills et al. 1996, Wisdom and Mills 1997). Hence, the form and complexity of the population model employed should be carefully considered.

Model selection must be based partially on the availability of data to parameterize the model. Unfortunately, demographic data are often difficult and expensive to obtain and can be quite scarce. For example, Green and Hiron (1991) reviewed current knowledge of demographic parameters for 1029 bird species that Collar and Andrew (1988) considered threatened. They found that estimates of age at first breeding, productivity, and survival were available for only 15 of the species. Clearly, it is desirable to collect local data when possible. However, often it will not be possible to obtain sufficient samples in the field for estimating key parameters for all species of interest. Intermediate situations will commonly exist where demographics are analyzed using published data for some parameters and local data for those variables thought to vary in important ways among locales.

Data requirements vary with the type and complexity of the demographic model. Population models can range from simple models (e.g., exponential population growth) to very complex models (e.g., individual-based, spatially explicit metapopulation models) (Burgman et al. 1993). Exponential growth models assume future growth will be a function of past growth. Hence they have relatively few parameters and can be useful when local data are limited. These models often ignore the demographic and spatial structure in the population. However, they may be adequate for modeling populations (1) with densities well below the environment's carrying capacity, and (2) into the near future when growth is not extreme and critical rates are not changing dramatically due to density changes (Burgman et al. 1993). Simple models can be quite enlightening (see examples in Eberhardt 1987, Burgman et al. 1993). A shortcoming of many simple models is that they do not indicate which aspects of demography (e.g., survival vs. reproduction) strongly influence population change.

More complex population models that incorporate age structure and employ reproduction and survival rates can be more instructive (e.g., Leslie matrix projections such as those of Hitchcock and Gratto-Trevor 1997). Even greater resolution can be obtained as subcomponents of reproduction (e.g., clutch size, nest success, etc.) or survival (e.g., overwinter survival, survival during migration, etc.) are included in models (Johnson 1994). If habitat-specific data are available, source-sink models (Pulliam 1988) can be used to identify those habitats most important to population persistence (Pulliam and Danielson 1991). Still more complex and difficult to parametertize, spatially explicit population models can be used to examine the effects of landscape configuration, dispersal ability, and metapopulation structure (Hanski and Gilpin 1991, Dunning et al. 1995). Finally, in the rare but desirable cases when adequate data are available, models can also incorporate population density, environmental variation, competitors, and/or predators (Starfield and Bleloch 1987, Burgman et al 1993, Johnson 1994).

Once a model has been chosen, analyses are conducted to estimate the probability of the population attaining an undesirable status within a specified time given the model's assumptions. Analyses can be for long or short time periods, and models can be deterministic or stochastic. If a stochastic model is used, one typically records the percentage of simulations that result in the population going extinct. It is also possible to estimate the population's growth rate and a confidence interval about the rate. Sensitivity and elasticity analyses can be used to evaluate the relative importance of different life history stages to the population's growth rate (Caswell 1990, Hitchcock and Gratto-Tre-

TABLE 3. Population growth rates for "most-at-risk" guild simulated in three habitat types in the Greater Yellowstone Ecosystem.

Habitat type	Birds fledged per nest†	Percentage of extinctions‡	Population growth rate (95% CI)
Aspen	1.15	0	1.11 (1.07–1.15)
Cottonwood	0.78	9.9	0.92 (0.89–0.96)
Lodgepole pine	1.36	0	1.22 (1.18–1.26)

† Number of female young fledged per nesting attempt (estimates from field data).

‡ Percentage of populations that went extinct during 50-yr simulations (n = 1000 simulations with starting populations of 100 juveniles and 100 adults).

vor 1997, Wisdom and Mills 1997). A wide array of literature (e.g., Caswell 1990, Tuljapurkar 1990, Burgman et al. 1993) and software (e.g., Legendre and Clobert 1995, Mills et al. 1996) is available for population analysis.

Greater Yellowstone Ecosystem example

Our pilot study in 1996 of bird demography in the GYE study area focused on the two habitats (aspen and cottonwood) that support the most species identified as at risk and on the most extensive habitat in the study area (late-seral lodgepole pine). Within these habitats, we estimated nest success for species with cup-nests within 10 m of the ground. This allowed us to collect nest success data on ~50 nests from 30 bird species, which included 13 of the 25 species designated as most at risk in Appendix A. The methods of Martin and Guepel (1993) were used to locate and monitor nests and estimate nest success following Hensler and Nichols (1981). We derived age-specific annual survival rates from published literature. These data were used to parameterize a stochastic model that incorporated age-specific survival rates and annually varying reproductive rates (non-age-specific) to estimate population change.

While we were able to obtain nest success data in the field, survival estimation was precluded because we did not have the resources to mark and relocate adequate samples of birds in multiple species and years (Brownie et al. 1985, Lebreton et al. 1992). Because we worked with migratory birds whose dispersal ability we assumed to be excellent and because necessary data were unavailable, our model did not incorporate dispersal data. Data limitations also prevented us from making our model spatially explicit. However, we were not deeply concerned about this because patch dimensions and landscape contexts were very consistent within each habitat type.

Sufficient samples were not obtained in 1996 to model individual species. Thus, we were not able to complete the Step 3 screening. Adequate data will often be lacking in real-world applications of the method. Here we take best advantage of current knowledge by performing a PVA for the guild of at-risk species that are most abundant in deciduous habitats. Included in this guild were American Redstart, Willow Flycatcher, Veery, Western Wood-Pewee, Orange-crowned Warbler, Least Flycatcher, Cedar Waxwing, MacGillivray's Warbler, Wilson's Warbler, Northern Waterthrush, and Common Yellowthroat. We estimated the number of female fledglings produced per nesting attempt in each of the three habitats, pooling data for all warbler-like species. We used our habitat-specific estimates of reproductive output from 1996 and allowed them to vary stochastically (normally distributed, 1 SD = 0.25) among years. We did not incorporate the effect of multiple nesting attempts into our model because we do not have data for this variable. We considered two age classes in the population (second-year [SY] and after-second-year [ASY]) and assumed equal reproduction for both age classes.

We used published estimates of survival estimates for ASY birds (0.54, Martin 1995) but could not find published data for survival of younger birds. We assumed that young birds do not survive as well as older birds. Therefore, in our model, 50% of fledglings survive to become SY breeders. Survival rates in the model did not vary by habitat or among years.

We estimated the population's average growth rate in the three habitats using the program ULM (Legendre and Clobert 1995). The average growth rate and extinction probability in each habitat was estimated based on 1000 Monte Carlo simulations (50 yr per simulation) (Table 3). Next, we used habitat maps of our area, field data for the density of this guild in each habitat type, field data for reproductive output per nest, and model output to estimate the following: (1) the proportion of the population in each habitat, (2) the proportion and (3) number of young produced in each habitat, and (4) the population growth rate across all habitats (Table 4).

The results suggest that, within the limits of the model and our assumptions, aspen and lodgepole pine forests act as population source areas (population growth rates exceed 1.0) for this guild, while cottonwood stands act as sinks (growth rate <1.0). This is likely the case because the intense human land uses in the

TABLE 4. Simulated source–sink dynamics of populations of birds in the "most-at-risk" guild occupying three habitat types in the Greater Yellowstone Ecosystem.

Habitat	Habitat area (ha)	Pairs/ha	Total pairs	Population growth rate	Annual net change in population size
Aspen	18 499	0.360	6660	1.11	733
Cottonwood	6265	0.773	4843	0.92	(−387)
Lodgepole pine	74 829	0.005	374	1.22	82
Total	99 593	...	11 877	...	428

landscapes surrounding the cottonwood forests favor high densities of nest predators and the brood parasitic Brown-headed Cowbird. Aspen are in a seminatural setting and have lower densities of nest predators and brood parasites.

These findings demonstrate the importance of demographic analysis when managing biodiversity. Distribution data alone would be misleading and indicate the need to maintain cottonwood in its current state as the key to maintaining the population. In reality, the demographic data indicate that aspen largely maintains the local population of this guild of species and that management actions should seek to preserve aspen stands and consider altering cottonwood forest in ways to promote improved nest success.

We emphasize that this preliminary analysis is based on a small data set and makes many simplifying assumptions. Based on what we learned about nest sampling in 1996, we initiated a more comprehensive nest-success study in 1997 (~500 nests were sampled). When this demographic work is concluded in 2000, we expect to have sufficient data to conduct similar analyses for each of the species identified as most at risk.

Step 4: Management Design

How can the results above be used to manage for important species and places? Several good guidelines have been published for conservation planning, implementation, and evaluation at local to regional scales (see Noss and Cooperrider 1994, Hunter 1996). These range from managing ecosystem processes to sustain biodiversity (Cissel et al. 1994), to maintaining habitats for several species within specific taxonomic groups (e.g., Hansen et al. 1993), to designs based on the demography of single species (e.g., Murphy and Noon 1992). DHP Analysis produces data sets that allow a combination of these approaches.

In the context of adaptive management (e.g., Walters 1986), our approach provides data and knowledge on key relationships between organisms and the local environment. These data sets include: biophysical features; distribution of species richness; distribution of abundance for species at risk; and distribution of population sources and sinks for species highly at risk. Such data provide a basis for devising alternative management scenarios. The data can also be used for parameterizing simulation models to evaluate the likely consequences of each scenario for habitat patterns, distributions of species abundance, and species population dynamics (e.g., Liu 1992, Hansen et al. 1993, 1995, White et al. 1997). After one or more scenarios have been implemented, the results of monitoring can be used to evaluate management success and to revise/refine the Dynamic Habitat and Population (DHP) Analysis.

The results of our approach are particularly useful for hierarchical management scenarios that seek to actively restore populations and habitats of species most at risk while maintaining key habitats and ecosystem processes to prevent other species from becoming at risk. Species most at risk may require habitat preserves, active management of habitats to restore habitat quality or abundance, control of amensal species, and/or ex situ measures such as captive breeding. This could be complemented by more of a coarse-filter approach that manages natural and human disturbances to maintain the range of habitat types required by species currently less at risk.

Greater Yellowstone Ecosystem example

It is beyond the scope of this paper to offer a comprehensive management plan for our study area. Instead, we sketch a potential management approach to illustrate the ways these data can be used. We set as objectives: (1) restoring/protecting population source areas for species most at risk; and (2) managing all habitats to prevent other native species from becoming at risk. Key data layers on biodiversity used in this effort included: richness of all species; richness of species moderately and highly at risk; and population source areas for the guild of at-risk species on which demographic analyses were conducted. We did not consider the feasibility (e.g., political, economic, social) of implementing the management strategies. Those would be key considerations for those managing the planning area. Our purpose is to present strategies aimed at preventing species extinctions.

Total species richness was extrapolated over the study area by applying parameters from a multiple regression equation to spatially explicit, digital data layers of predictor variables. The equation was derived from the field studies in 1995 and 1996. Predictor variables included cover type, seral stage, and elevation. The model explained 67% of the variance in the data and was statistically significant at the $P < 0.0001$ level.

Richness of at-risk species was mapped by predicting probability of presence for individual species over the study area based on binomial logistic regression functions. Digital maps of individual species presence ($\geq$50% probability of occurrence) were integrated to estimate the richness of these at-risk species. Two logistic regression models were compared for each of the at-risk species, one with cover type and elevation as predictor variables and one considering only cover type. The model with the best fit to the data, as evidenced by the lower AIC value (Akaike 1973, Burnham and Anderson 1992), was used in the extrapolations (Appendix B).

The species most at risk had highest projected richness in cottonwood, aspen, and willow habitats, especially those at lower elevations (Fig. 4A). Fourteen of the seventeen species classified as at risk were predicted to be present in these three deciduous habitats. Some of these species were also predicted to be present in other habitat types. However, bird census data revealed that most of these species were substantially

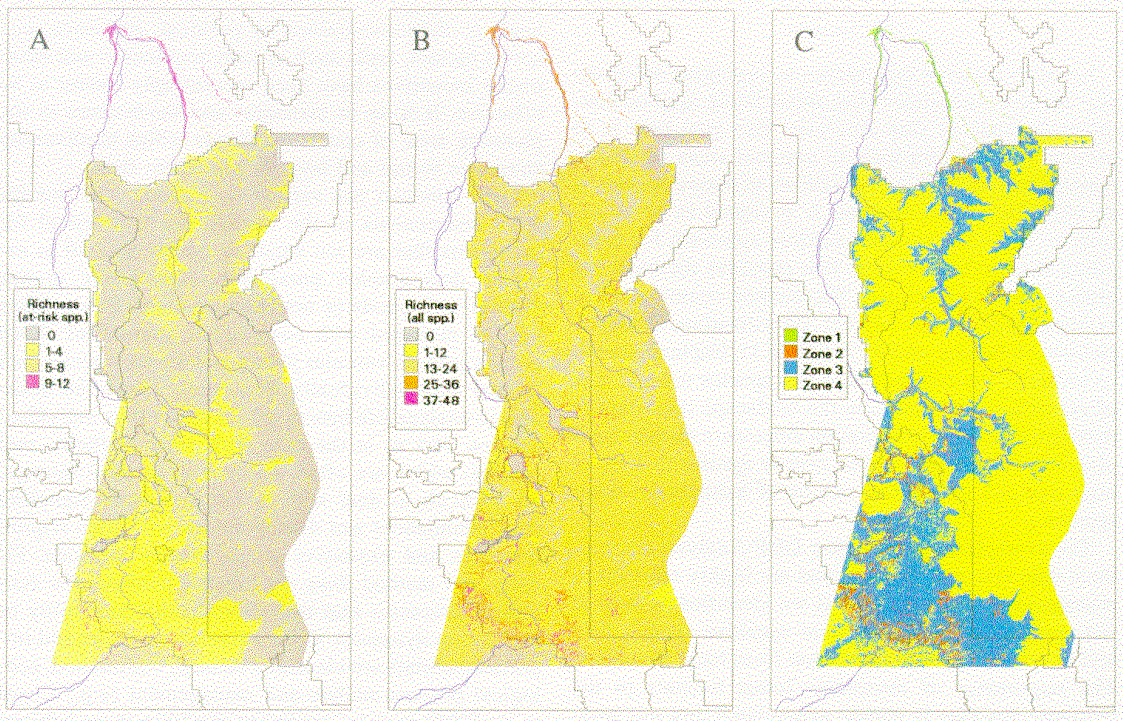

FIG. 4. Maps of species richness and hypothetical management plan across the study area: (A) Richness of the 17 species identified as most at risk in Screening 2. Richness was estimated by overlaying maps of presence developed from logistic regression for each of the 17 species. (B) Map of richness for all species sampled in the study area developed from a multiple regression equation including cover type and elevation as predictor variables. (C) Hypothetical management zones across the study area. See *Step 4: Management design* for a description of management directives for the zones.

more abundant in the deciduous habitats. There were three exceptions. Black-backed Woodpecker was found only in seedling/sapling lodgepole pine following wildfire and in old-growth lodgepole pine habitats, both at lower elevations. Olive-sided Flycatcher occurred primarily in seedling/sapling lodgepole pine following clearcutting, and mature lodgepole pine habitats, both at lower elevations. And Brewer's Sparrow was found only in sage habitats.

Total species richness somewhat mirrored the pattern of richness of the species at risk (Fig. 4B). Richness increased from sage and herbaceous, to high-elevation conifer, to low-elevation conifer, to the three deciduous habitats.

Based on these results, we derived a management plan with four zones (Fig. 4C). Zone 1 includes habitats that have the potential to be restored as source areas for the guild of at-risk species specializing on deciduous habitats. This guild reaches peak densities in cottonwood habitats. Yet reproductive success is very low in this habitat, likely due to the nest predators and brood parasites attracted by the surrounding land-use activities. The management strategy here is to reduce grazing, crop agriculture, and rural residential development through education programs for land owners, tax incentives, land acquisition, and county zoning. Cottonwood regeneration depends upon exposed fine sediments created by flooding. Thus, river bank stabilization would be discouraged.

Likely current population source areas (aspen and willow stands) compose Zone 2. The primary strategy here is to prevent reduction of the area and quality of these habitats. On public lands, grazing, road-building, and wetland drainage would be restricted, and prescribed fire and silviculture would be used to restore aspen stands that have senesced due to herbivory and lack of fire. On private lands, landowner education and tax incentives would be recommended.

Zone 3 includes lower elevation conifer stands. Conifer-associated bird species reach peak abundance and richness in these stands, yet they are often most heavily subjected to logging, grazing and road building. The management strategy is to tailor silviculture and prescribed fire to biophysical gradients to maintain the full range of conifer seral stages across the elevational gradient (see Hansen and Rotella 1999).

The remaining habitats in the study area are within Zone 4. This zone would be managed to maintain the current range of cover types and seral stages. As mentioned above, management activities in all zones are best done in an adaptive management context where new knowledge is gained with each management implementation.

Discussion

Local to regional approaches to managing biodiversity are less formalized than those being applied continentally such as Gap Analysis. Our goal here is to present a method for local to regional areas where the maintenance of viable populations of native species is an objective. DHP Analysis is designed to be an effective, cost-efficient, and flexible approach for compiling data and knowledge that provides the basis for biodiversity management. The method combines three existing approaches: Species Prioritization; Dynamic Habitat Modeling; and PVA (Table 1). Implemented in its entirety, the method identifies species most at risk of extinction, and places in the landscape important to these species. This information empowers management planning to maintain and/or restore species that are at high risk and to prevent erosion of habitats for other species.

The example illustrated how DHP Analysis can produce data sets and insights that are highly relevant to management. The species that we identified as most at risk are not currently on local sensitive-species lists and have received little attention from local managers. The importance of deciduous forest habitats in the Northern Rockies is widely appreciated, but our analysis is unique in documenting the small proportion of the landscape that is occupied by these deciduous habitats. The analysis also revealed that the abundances of many species are correlated with elevation such that species abundances are highest at lower elevations. The population modeling suggested that some of these low-elevation "hot spots" for bird abundance and diversity are likely population source areas for the species identified as most at risk. However, hot spots that are surrounded by intense human land use appear to be population sinks for these species. This disparity between high population abundance in these hot spots and low predicted population viability demonstrates the need to integrate coarse- and fine-filtered approaches in conservation planning. While our example deals with birds, our approach can be used for any taxonomic groups for which adequate data can be obtained.

The GYE management plan can be improved as research continues. Additional predictor variables involving climate, topography, and soils may allow development of more accurate projections of species abundance across the planning area. Also, larger sample sizes on nest success will allow us to conduct PVAs individually on the species identified as most at risk. Even at its present state, however, our study is one of the most comprehensive in the region and we recommend that local managers consider the proposed plan as a starting point. In being based on ongoing research, the example demonstrates a strength of DHP Analysis. It takes advantage of best current knowledge, and the approach can be redone and management modified as knowledge is improved. While management on private lands is often constrained by political, economic, and social factors, tools such as land acquisition and landowner incentives have been increasingly shown to be effective. It is up to managers and landowners in the planning area, of course, to decide which biodiversity strategies to use and how to implement them.

DHP Analysis has various limitations. The fine-filtered components of the method are impractical for organisms that are too small or poorly studied to estimate demographic parameters. Taxonomic groups such as arthropods or nonvascular plants can perhaps best be managed with coarse-filter approaches. Even groups such as vascular plants may be too species rich to deal with individually. Sometimes it may be desirable to analyze life history guilds rather than individual species. Just as is the case with other methods, rare species, which are often the ones of greatest interest, are difficult to deal with in our approach. Sampling their abundances and demographies will often require intensive and expensive single-species methods. Finally, our method does not directly consider the ecological processes that may drive habitat suitability or population dynamics. Once vulnerable species and important habitats are identified through our method, ecological process studies and management (e.g., Cissel et al. 1994) may be needed to maintain these habitats and species.

Despite these limitations, DHP Analysis offers promise of helping to resolve the biodiversity manager's dilemma in choosing between coarse- and fine-filter approaches. It provides a conceptual framework by which managers working at different spatial scales can link their efforts to efficiently maintain species. For example, Gap Analysis (Scott et al. 1993) is identifying regions across the U.S. that contain many species and are not well protected at present. Local managers within these regions can use our approach to develop site- and species-specific management strategies. Even managers of places not designated as of high national priority can use the method to reduce the chance of local extinctions, which should contribute to minimizing range-wide extinctions.

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APPENDIX A

Data used in Screening 2. Variables are defined in Table 3. For brevity, species in Screening 2, Quintiles 1 and 2 are not shown.

Species	Population size	Habitat area (ha)	Predator susceptibility	Nest parasite susceptibility	Reproductive effort	Screening 1 quintile	Screening 2 quintile
Yellow Warbler	6 081	74 503	0.00	0.00	4.5	2	3
American Crow	3 264	23 885	0.00	0.00	6.5	4	3
Barn Swallow	26 298	132 546	0.00	0.00	11	4	3
Clark's Nutcracker	9 207	6 340	0.00	0.00	7	2	3
Common Raven	24 412	14 627	0.00	0.00	9	2	3
Fox Sparrow	5 224	70 708	3.46	0.00	5	1	3
Grasshopper Sparrow	157	53 109	0.00	0.00	5.5	5	3
Green-tailed Towhee	5 725	16 574	0.16	0.99	8	3	3
Northern Rough-winged Swallow	2 300	6 340	2.97	0.00	4	1	3
Three-toed Woodpecker†	4 440	10 941	0.54	0.00	3	5	3
Western Tanager	2 830	65 026	0.40	0.00	9	5	3
Black-backed Woodpecker†	24 734	9 202	0.21	0.22	4	2	3
Brewer's Blackbird	7 217	35 089	0.36	0.00	3.5	5	3
Evening Grosbeak	786	62 946	1.37	0.00	8	4	3
Swainson's Thrush	21 938	53 109	0.00	0.00	5.5	2	3
Warbling Vireo	42	6 340	0.00	0.00	5.5	4	3
Common Yellowthroat†	32	16 574	0.00	0.00	9	1	4
Lazuli Bunting	1 913 462	560 888	0.10	0.00	9	2	4
Northern Waterthrush†	21 439	22 914	0.50	0.31	4.5	1	4
Olive-sided Flycatcher†	6 324	9 202	0.00	0.00	4.5	2	4
Wilson's Warbler†	2 397	214 005	4.97	0.00	3.5	5	4
Black-headed Grosbeak	2 229	68 984	3.08	2.91	10	3	4
Blue Grouse†	114	14 627	8.94	0.00	5	3	4
Brewer's Sparrow†	22 978	293 442	0.83	0.00	9	5	4
Dusky Flycatcher†	708	537 806	11.37	0.00	4	3	4
House Finch	1 384	6 340	0.66	0.00	9	5	4
MacGillivray's Warbler†	28 865	9 202	0.70	0.00	3.5	5	4
Mourning Dove	104	43 238	7.53	0.00	10	1	4
Ruffed Grouse†	833	19 228	1.67	5.86	3.5	3	4
Steller's Jay†	337	222 402	17.59	0.00	8.5	4	4
Williamson's Sapsucker	3 175	16 574	0.13	1.13	3.5	4	4
Cedar Waxwing†	92 388	14 627	0.31	0.00	10	1	5
Grey Catbird	2 341	19 744	0.26	0.00	5	4	5
Least Flycatcher†	2 178	21 175	0.47	0.00	5	3	5
Northern Oriole†	19	6 340	50.00	103.00	3.3	3	5
Orange-crowned Warbler†	1 483	6 340	0.00	0.00	10	1	5
Red-naped Sapsucker†	41 391	209 404	0.46	0.00	4	4	5
Violet-green Swallow†	416	6 340	0.00	0.00	4.5	4	5
Hammond's Flycatcher†	22 558	226 197	0.86	0.00	8	4	5
Red-winged Blackbird	529	375 234	28.84	0.00	7	2	5
Western Wood-Pewee†	1 184	191 246	0.00	0.00	4	3	5
American Goldfinch	27	9 202	13.00	0.00	9	1	5
Bobolink†	2 170	436 739	0.00	0.00	5.5	2	5
Common Grackle	10 293	413 646	2.21	0.00	3	3	5
Rufous-sided Towhee†	103 419	209 404	0.21	0.00	9	2	5
Veery†	27 203	401 788	0.62	0.00	7	3	5
Willow Flycatcher†	2 096	22 914	0.56	3.29	8	5	5
American Redstart†	285	40 800	2.85	0.00	5.5	5	5
Red-eyed Vireo	75 459	225 402	0.06	0.06	7	4	5
Eastern Kingbird	7 176	250 094	2.53	0.00	3.5	4	5

† Species considered most at risk of extinction in the study area.

APPENDIX B

Results of logistic regression analyses predicting presence of each of the at-risk bird species.

Species	Number of observations	Model	L-ratio chi-square value	L-ratio *P*	Maximum adjusted R^2	Concordance (%)	Fit†
American Redstart	54	Cover + Elev.	49.4	0.0001	0.82	98.8	0.92
Willow Flycatcher	173	Cover + Elev.	49.4	0.0001	0.79	97.9	0.55
Veery	112	Cover + Elev.	31.8	0.0002	0.55	93.2	0.79
Western Wood-Pewee	235	Cover + Elev.	50.1	0.0002	0.63	94.0	0.04
Red-naped Sapsucker	49	Cover + Elev.	45.4	0.0002	0.63	94.1	0.97
Orange-crowned Warbler	74	Cover	23.7	0.0025	0.77	80.3	1.00
Northern oriole	25	Cover	33.1	0.0001	0.71	97.0	0.93
Least Flycatcher	110	Cover	33.0	0.0001	0.71	95.7	0.93
Ruffed Grouse	100	Cover	20.1	0.0100	0.30	71.2	1.00
MacGillivray's Warbler	88	Cover + Elev.	40.4	0.0001	0.52	89.5	0.21
Brewer's Sparrow	86	Cover	29.7	0.0002	0.50	92.4	0.93
Wilson's Warbler	102	Cover	36.5	0.0001	0.50	84.6	1.00
Olive-sided Flycatcher	87	Cover + Elev.	23.3	0.0055	0.32	80.2	0.20
Northern Waterthrush	146	Cover	23.3	0.0055	0.7	80.2	0.93
Common Yellowthroat	21	Cover	74.3	0.0001	0.75	95.8	0.93
Dusky Flycatcher	51	Cover + Elev.	71.9	0.0001	0.69	92.8	0.42
Black-backed Woodpecker	16	Cover + Elev.	24.1	0.0040	0.54	94.7	0.93

Notes: Column headings are: species; number of observations; the best model; estimated chi-square value of the model with the likelihood-ratio test; estimated significance of the model with the likelihood-ratio (L-ratio) test; the maximum adjusted R^2, which estimates what proportion of the maximum possible likelihood value was achieved; concordance, which is the estimate of the model's predictive ability (the percentage of all possible pairs of observations where the observation with the lower observed response value also had the lower predicted response values); and the assessed fit of the model with the Hosmer-Lemeshow test (values >0.1 indicate adequate fit). Species that were observed <15 times during the 1995–1996 sampling and species showing nonsignificant L-ratio values were omitted from the analysis.

† Hosmer and Lemeshow goodness-of-fit test.