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PROJECTING WILDLIFE RESPONSES TO ALTERNATIVE FUTURE LANDSCAPES IN OREGON'S WILLAMETTE BASIN

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Abstract. Increasingly, environmental quality is becoming recognized as a critical factor that should constrain land use planning. One important measure of a landscape's quality is its capacity to support viable populations of wildlife species. But the ability of land managers to balance conservation with other competing objectives is limited by a shortage of methodologies for assessing landscape quality. In response to this shortage, the research community has begun developing a variety of multispecies, landscape-level, assessment models. Useful models must strike a balance between parsimony and biological realism and must be designed to make the most of limited life history data. This paper applies two such assessments to an examination of wildlife responses to scenarios of landscape change within Oregon's Willamette River Basin. The study uses GIS maps of pre-European settlement and circa 1990 habitat conditions, and three possible realizations of how the Basin might appear in the year 2050. Our simpler assessment generated statistics of landscape change from the GIS imagery and species-habitat relationships for all 279 amphibian, reptile, bird, and mammal species in the basin. Our more complex assessment used an individual-based life history simulator to estimate population sizes for a small subset of this fauna. These two assessments offer complementary kinds of information about wildlife responses to landscape change: estimates of habitat changes for a large number of species representing a region's biodiversity, and estimates of changes in the persistence of populations of key species. We found both good and poor correlations between our two assessments, depending upon the species and landscape. Both assessments agreed in their overall ranking of the landscapes' quality for wildlife. In most cases, the percentage change in habitat quality underestimated the percentage change in population size. In a few cases, small gains in habitat quality were accompanied by very large increases in wildlife populations. We attribute discrepancies in our two assessments to the influence habitat fragmentation had on our individual-based model. As such, our study provides a methodology for separating the influences of habitat quality and quantity from those of habitat pattern.

Key words: *alternative future landscape; habitat change; habitat model; landscape change; model comparison; PATCH; population viability analysis; simulation model; wildlife model.*

INTRODUCTION

This paper examines the implications for wildlife of landscape changes that may occur within Oregon's Willamette River Basin (WRB) over the next 50 years. The larger project, of which we are a part, was designed to provide managers and policy makers with information essential to making well informed land use planning decisions (Baker et al. 2004). The focal point of this study, and of the project as a whole, was a set of geographical information system (GIS) maps that displayed anticipated landscape changes through time for the WRB (Hulse et al. 2004). The WRB GIS maps

included pre-European settlement ("historic") and circa 1990 habitat coverages, and three alternative depictions of future landscape conditions referred to subsequently as "alternative futures." The alternative futures are realistic depictions of WRB conditions in 2050 under three different assumptions for basin-wide land use planning trends. The different components of this project examined the significance of these alternative future scenarios for a diverse array of ecological endpoints. Our study explored the consequences of the landscape modifications for terrestrial wildlife populations.

There is no accepted general methodology for predicting the consequences for wildlife populations of landscape change (Doak and Mills 1994, Schumaker 1996, Fahrig 1997, 1998, Ruckelshaus et al. 1997). Here, we compare and contrast two assessment approaches that differ greatly in their scope and com-

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plexity. Our simpler assessment was based upon descriptive statistics applied to an entire fauna. Our more complex assessment used an individual-based model to carefully examine a subset of this fauna. In absolute terms, both of our assessments were simplistic in that they ignored environmental stochasticity, most behavior, interspecies interactions, and many anthropogenic stresses. However, while our first assessment uses only habitat maps and species-habitat preference data, the second also requires species' area needs, survival, reproduction, and movement information. When the two assessments agreed, a case could be made that the simpler one was sufficient, and that habitat quality and quantity were the key predictors of population trends. When our assessments disagreed, we believe the discrepancy could be attributed principally to the effect habitat fragmentation had on the individual-based model's estimates of species performance.

The impacts of habitat fragmentation on wildlife are frequently documented (Thomas et al. 1990, Chen et al. 1992, Fahrig and Merriam 1994, McGarigal and McComb 1995, Brooker et al. 1999, Villard et al. 1999, Burke and Nol 2000, Foppen et al. 2000, Murphy 2001), but it does not follow that models capturing the influence of landscape pattern are generally superior to those that do not. Limitations in data and in understanding often make simpler analyses preferable to complex ones (Mooij and DeAngelis 1999). And simple models, in spite of their obvious omissions, are easier to use, and tend to better illuminate general principles. Complex models provide more opportunities to misrepresent mechanisms, and suffer increasingly from error propagation (Conroy et al. 1995). Our intent here is not to advance a specific analytic approach, and we do not provide accuracy estimates or argue in favor of one methodology vs. another. Rather, our goal is to provide two contrasting assessments of the significance of landscape change for an array of wildlife species, and to illustrate the commonalities and differences among the results.

Both our simple and complex assessments rely principally on species-habitat relationships. These numerical estimates of the importance of various habitats for wildlife species have long been a subject of ecological research, in large part due to their importance as management tools. Species-habitat relationships have been broadly applied (Edwards et al. 1996) in studies ranging from simple assessments (Verner et al. 1986, Morrison et al. 1992), to spatially explicit descriptions of animal distributions (Scott et al. 1987), and the development of gap analysis models (Scott et al. 1993). Species-habitat relationships are often used to predict species presence or absence, but their simplicity can result in models having poor predictive power (see, for instance, Bolger et al. 1997). White et al. (1997) extended the approach by using species-habitat association models, maps of proposed future habitat distri-

butions, and area requirements for mammals, birds, amphibians, and reptiles to assess risks to biodiversity from anticipated landscape change. For the present study, species-habitat relationships were developed for each of 279 amphibian, reptile, bird, and mammal species assumed to occur now, or in the past, in the Willamette River Basin.

Our simple assessment coupled GIS imagery to species-habitat relationships for the purpose of developing statistics of landscape change for an entire set of non-fish vertebrate species. We use change in the amount of habitat for all resident breeding terrestrial vertebrate species as an indication of the change in species biodiversity. This habitat-based assessment, with its focuses on aggregate statistics of change rather than on the performance of specific populations, has the advantage of being tractable; computing persistence individually for the same set of species would be impossible due to a general lack of life history data. A key assumption in this assessment is that the errors inherent in using habitat as a surrogate for viability average out across a large enough array of species.

Our more complex assessment used an individual-based spatially explicit population model (SEPM) to couple species' habitat needs to their survival, reproduction and movement rates. The added sophistication of SEPMs (Dunning et al. 1995) makes it possible to study source-sink and metapopulation dynamics (Pulliam 1988, Pulliam and Danielson 1991, Doak 1995, Moilanen and Hanski 1998, Moilanen 1999, Wiegand et al. 1999, Foppen et al. 2000), and to perform population-viability analyses (Possingham and Davies 1995, Lindenmayer and Possingham 1996, Beissinger and Westphal 1998, Forsys and Humphrey 1999). SEPMs such as ours use and are sensitive to species-habitat associations and area requirements. They also require estimates of demographic parameters and movement characteristics. Because these values can be unattainable or inaccurate, an accumulation of parameter uncertainties can render SEPMs vulnerable to error propagation (Conroy et al. 1995). The ramifications for model performance of limitations in the accuracy and availability of parameter estimates is an active area of research (Pulliam et al. 1992, Kareiva and Wennergren 1995, Wennergren et al. 1995, Fahrig 1997, 1998, Ruckelshaus et al. 1997, 1999, Mooij and DeAngelis 1999, South 1999).

METHODS

Study area and scenarios

The Willamette River Basin (WRB) encompasses 29 728 km² between the Cascade and Coast Range Mountains in western Oregon, and ranges in elevation from 1 to 3200 m above sea level. Cool, wet winters favor the growth of conifer forests in the uplands, which cover about two-thirds of the basin. Prior to Euro-American settlement (~1850), much of this co-

niferous forest was late-successional old growth (>200 yr old) with only scattered patches of younger forests. Estimates of the extent of old growth forest in western Oregon and Washington prior to settlement range from 60 to 75% of the forested area (Andrews and Cowlin 1940, Booth 1991, Bolsinger and Waddell 1993, National Research Council [NRC] 2000). As a result of forest harvesting, by 1990 <20% of WRB uplands supported conifer forest >200 years of age, based on analysis of satellite imagery (Cohen et al. 2001, Hulse et al. 2004). Concerns about the loss of old growth and associated impacts on wildlife vs. the dependency of local economies on continued intensive forest harvest are evidenced by the controversy surrounding the Northwest Forest Plan (Forest Ecosystem Management Assessment Team 1993).

Vegetation changes have been even more dramatic within the lowland Willamette Valley ecoregion. Historically, a diverse bottomland forest of black cottonwood, Oregon ash, alder, and other riparian species extended 2–10 km wide along the length of the Willamette River. Only 20% of that area is forested today, with the remainder converted to agriculture and human development. Portland, Salem, Eugene–Springfield, and Corvallis—the major human population centers in the basin—all occur along the river. Elsewhere in the valley, fires set regularly by Native Americans maintained oak savanna (principally Oregon white oak) and open grasslands (Boyd 1986). Extensive land conversion for human use, together with the invasion of shrubs and trees following fire suppression, have led to near 100% loss of some of the unique habitats that evolved under the presettlement fire regime. It is questionable whether any true oak savanna/prairie remains to this day. An estimated 99% of the wet prairie and 58% of emergent wetlands have been converted to agricultural and urban uses (Titus et al. 1996). The expected doubling of the human population in the Willamette Basin over the next 50 years, to nearly four million people, will place added pressure on the remaining native habitats and associated wildlife populations.

We examine here five different depictions of the Willamette river basin, each consisting of a raster GIS map containing 33 million 30-m pixels. These data sets are described in detail by Hulse et al. (2004). The “Circa 1990” image shows the basin’s land cover as it appeared in 1990 (approximately), and was created from an array of data sources using a classified Landsat Thematic Mapper satellite image as a base map. Our “Historic” image shows the basin’s land cover as it appeared prior to settlement by Europeans (~1850). This data set was compiled in large part using Government Land Office survey maps and records of land use practices over the past 150 yr. In addition, Hulse et al. (2004) developed three maps of possible land cover conditions in the year 2050 reflecting potential changes in urban and rural development, agriculture, forestry

practices, and natural resource management. These “alternative future” landscapes are referred to as “Plan Trend 2050,” “Conservation 2050,” and “Development 2050.” The Plan Trend 2050 image captures what we expect would result 50 yr into the future if existing land use plans are implemented as written and current trends continue. Conservation 2050 and Development 2050 depict the consequences, respectively, of shifts in land use planning towards the preservation of a broad array of habitats, versus a more market-oriented approach with fewer environmental regulations. The most significant feature of the alternative future maps is their plausibility. These images bracket the range of future conditions that can be realistically expected in the WRB in the year 2050, according to the stakeholder groups with which we interacted (Hulse et al. 2004). They are not limiting cases that assume unrealistic shifts in policy. As a result, the maps of circa 1990 conditions and the three alternative futures do not differ dramatically from each other. Our historic (presettlement) map differs from the other four GIS data sets in that its construction did not begin with a satellite image, and it therefore does not contain the fine-grained detail associated with remotely sensed imagery. While this surely reflects circa 1850 conditions to a large extent, some amount of habitat fragmentation likely existed, and its omission may cause our analyses to overestimate the quality of the presettlement landscape for some wildlife species.

Species–habitat relationships

Four expert panels were assembled to develop wildlife species–habitat relationships for each of the 279 bird, mammal, amphibian, and reptile species thought to breed in the WRB at present, or to have occurred at the time of first Euro-American settlement. Thirty-four habitat types were defined based on the 64 land use/land cover classes used to characterize each WRB scenario (Hulse et al. 2004). The need to simultaneously examine so many different organisms made it impossible to further refine these habitat definitions on a species-by-species basis. Each species was assigned to one or more of the 34 habitats, using a suitability rating on a scale of 0 to 10 that represented the relative preference of the species for breeding in the habitat (Table 1). Ratings greater than or equal to five were intended to imply that the habitat, if present in sufficient amount, would have the potential to support a viable population of the species. These initial ratings were then modified by one or more of 50 adjacency rules that adjusted ratings up or down to reflect the importance of nearby features, such as water or houses, on habitat suitability. Finally, species were constrained to a geographic range within the basin defined by the intersection of ecoregions (Clarke et al. 1991), elevation ranges, or one or more of 65 grid cells of 650 km² in size representing locations of occurrence. Habitat outside a species’

TABLE 1. Example species–habitat relationships, adapted from White et al. (2002).

Landscape class	Blue Grouse†	Douglas squirrel‡	Oregon slender salamander§	Red fox	Western Meadowlark¶	Western pond turtle#
Conifer 0–20 yr	2	2	0	4	0	0
Conifer closed 21–40 yr	3	7	2	4	0	0
Conifer closed 41–60 yr	8	8	4	4	0	0
Conifer closed 61–80 yr	10	8	4	4	0	0
Conifer closed 81–200 yr	9	9	10	2	0	0
Conifer closed 200+ yr	7	10	10	1	0	0
Mixed forest closed	5	7	4	5	0	0
Hardwood closed	3	1	0	8	0	0
Conifer semiclosed upland	5	6	3	4	0	0
Mixed forest semiclosed upland	4	6	2	6	0	0
Hardwood semiclosed upland	0	1	0	9	0	0
Tree open upland	3	5	0	10	0	5
Oak savanna	0	0	0	10	9	7
Shrub dry, tree open, semiclosed, valley	0	0	0	10	2	5
Shrub wet valley	0	0	0	4	0	0
Christmas trees	0	1	0	4	2	0
Orchards, hybrid poplar	0	1	0	0	0	0
Grass short	0	0	0	3	0	4
Grass natural	0	0	0	10	10	10
Grass tall	0	0	0	6	3	5
Bare, burnt, fallow	0	0	0	0	0	5
Seasonal wetlands	0	0	0	0	2	0
Built mid density	0	3	0	2	0	0
Built low density	0	2	0	4	0	2

Notes: The numbers are habitat weights indicating the importance of each landscape class for six example species. Weights ranged between zero and 10. To conserve space, 10 landscape classes were removed from the table since they held zeros for all six species.

† *Dendragapus obscurus*.

‡ *Tamiasciurus douglasii*.

§ *Batrachoseps wrightii*.

|| *Vulpes vulpes*.

¶ *Sturnella neglecta*.

Clemmys marmorata.

range was not included in the analyses. These species lists, habitat definitions, and ancillary data are described in detail in White et al. (2002). Both the habitat-based and individual-based modeling assessments described here assume that only breeding habitat is limiting.

Simple habitat-based assessment

Using the species–habitat relationships described above, we calculated aggregate statistics of habitat change among scenarios for all 279 terrestrial vertebrate species as an index of effects on wildlife biodiversity. The process starts by calculating a final habitat score at each location (data pixel) for each species in each landscape from the suitability ratings, adjacency rules, and geographic range for the species. From the maps of habitat scores we estimate the total amount of habitat for a species as the sum of all the scores across the landscape. We then calculated the percentage change in habitat for each species relative to Circa 1990 for the three future landscapes and for the Historic landscape. Finally, the median of the percentage changes for different groups of species was used as a summary statistic. The median was chosen as a robust measure of central tendency because of the skewed distributions of percentage changes. The approach used here

is a modification of that developed in White et al. (1997). The groups of species analyzed were native amphibians, reptiles, birds, and mammals separately, all native nonfish vertebrate species taken together, species introduced to the WRB, species extirpated from the WRB, and rare species. This last group was defined as those species with state conservation ranks of S1, S2, or S3, as determined by the Oregon Natural Heritage Program.⁵ In addition to median percentage change in habitat, we also computed the percentage of species that had increases or decreases in habitat. This indicator may be more closely related to biodiversity since it is expressed in proportions of total species numbers. The indicator is reported as the number of species that had increases in habitat minus the number that had decreases, as a percentage of the total. It therefore ranges between plus and minus 100%, with zero representing a neutral effect.

Parameter values for the complex model

The PATCH model (described in the next subsection), which we used for our analyses of population dynamics, is an individual-based females-only demographic simulator designed for terrestrial, territorial,

⁵ URL: <<http://www.abi.org/nhp/us.or>>.

vertebrate species. However, some of the species modeled here (e.g., coyote, red fox) are not technically territorial, and a home range was used in place of a territory. The parameter requirements of this model guided our data collection efforts. Of the 279 terrestrial vertebrate species described above, 153 are birds and 68 mammals. Fifty-three of these bird species and 24 mammal species were excluded because they either rarely breed in the WRB, are nonterritorial, communal, or colonial nesters (e.g., herons, swifts, and swallows), have very small territories (e.g., voles and shrews) or restricted movement patterns (mostly riparian obligates), which make them poorly suited for the PATCH model. An extensive literature search was conducted to obtain the life history parameters needed for PATCH, including territory size, juvenile and adult survival and reproductive rates, and maximum dispersal distance, for as many of the remaining bird and mammal species as possible (Bigger and Vesely 2000). Data from the WRB was assigned top priority. When satisfactory local references could not be found, we searched for parameter values from studies in Oregon (first) and the Pacific Northwest (second). If values from within the region were not available, data were then prioritized based jointly on a study area's similarity (e.g., climate or habitat types) and proximity to the WRB. The primary information source for birds was *The Birds of North America* series (volumes used are cited separately) and its bibliography. The primary source for mammals was *The Land Mammals of Oregon* (Verts and Carraway 1998) and associated bibliography.

Territory size was defined as the area actively defended during the breeding season. For studies reporting distance to the nearest neighboring nest, territory size was estimated as the area of a circle centered on the nest using one-half of the nearest-neighbor distance as the radius of the circle. Survival and reproductive rates were collected in the form of a Leslie matrix (Leslie 1945). Fecundity was recorded as the number of female offspring per female, per year, to reach the dispersal stage. In two instances, direct measures could not be located in the literature, and fecundity was then computed as one-half the product of mean clutch size and nestling survival rate, assuming a 50:50 sex ratio at birth. Survival rates were obtained preferentially from studies that followed individuals. In most cases, data for two stage classes (juvenile and adult) were collected and used in the Leslie matrix. Occasionally, three stage-classification data (juvenile, subadult, and adult) were available. Maximum dispersal ability was taken preferentially from data on females. Male maximum dispersal was used if female dispersal was unavailable. Often multiple values were available for a parameter and, depending on the nature of the values, they were treated in different ways. If a range of values was provided, the midpoint of the range was used. When a series of values or estimates from several dif-

ferent sources were available, the mean was used. Each reference was carefully checked to ensure the data were appropriate for our purposes. Our efforts resulted in data sets sufficient to run PATCH for 12 bird and five mammal species. Table 2 provides a list of the sources from which we obtained input parameters for the PATCH model. The species' life history parameters we actually used in the model are displayed in Table 3.

Complex individual-based assessment

PATCH (Schumaker 1998) stands for a program to assist in tracking critical habitat. The model reads GIS habitat maps, and is parameterized using species-habitat preferences, territory size, survival, and fecundity information in the form of population projection matrices (Leslie 1945, Lefkovitch 1965, Caswell 1989, Gotelli 1995), and estimates of movement ability and behavior (Fig. 1). PATCH is a females-only model capable of simulating environmental stochasticity and dynamic landscape change (neither of which were included in this study). PATCH simulations always incorporate demographic stochasticity, which results from the model's use of a random number generator to evaluate the outcome of individual survival and reproduction decisions. The model's outputs include various measures of population size, projected habitat occupancy and movement patterns, and estimates of the importance of each territory-sized parcel of habitat for the modeled population.

PATCH's life cycle begins with survival and then breeding events. Next comes the optional movements of adult animals (adult breeders stay in good breeding habitats), the mandatory dispersal of the juveniles, and finally a census is taken (Fig. 1). The process then begins again the following year. All mortality is collapsed into the single evaluation that takes place at the start of a year; there is no additional mortality associated with the movement processes. The results presented here were obtained from between one and 50 replicate simulations per species-landscape combination. A large number of test simulations were performed for each species to assess the variability in population size resulting from the model's incorporation of demographic stochasticity, and from the randomness inherent in the movement process (the simulations described here did not include environmental stochasticity). For each species, a number of replicates was selected that provided an accurate estimate of the mean population size (in the presence of demographic and movement-based stochasticity) but that did not increase the run time beyond what was necessary. The number of replicates typically decreased as population sizes increased because large population sizes had the effect of reducing overall variability. Because our simulations lacked environmental stochasticity, 10 replicate simulations were adequate in most cases. The number of years per simulation also varied by species, and

TABLE 2. Sources of the life history parameters used to conduct PATCH simulations for the 17 wildlife species examined.

Species	Data sources
Black-capped Chickadee, <i>Poecile atricapillus</i>	Odum (1941, 1942), Nickell (1956), Brewer (1963, 1978), Smith (1967, 1990, 1993), Glase (1973), Weise and Meyer (1979), Kluyver (1991), Dunning (1993)
Blue Grouse, <i>Dendragapus obscurus</i>	Boag (1966), Redfield (1975), McNicholl (1978), Armleder (1980), Jamieson and Zwickel (1983), Zwickel (1983, 1992), Zwickel et al. (1983)
Bobcat, <i>Lynx rufus</i>	Robinson and Grand (1958), Bailey (1974), Toweil (1986), Lariviere and Walton (1997), Verts and Carraway (1998), Sutherland et al. (2000)
Cooper's Hawk, <i>Accipiter cooperii</i>	Craighead and Craighead (1956), Henny and Wight (1972), Reynolds and Wight (1978), Reynolds (1989), Rosenfield and Bielefeldt (1993)
Coyote, <i>Canis latrans</i>	R. Chesness and T. Bremicker (<i>unpublished manuscript</i>), Nellis and Keith (1976), Bekoff (1977), Kennelly (1978), Verts and Carraway (1998), Sacks et al. (1999)
Douglas squirrel, <i>Tamiasciurus douglasii</i>	Smith (1968), Koford (1982), Gurnel (1987), Larsen and Boutin (1994), Verts and Carraway (1998), Steele (1999)
Gray Jay, <i>Perisoreus canadensis</i>	Walley (1981), Shank (1986), Strickland (1991), Strickland and Ouellet (1993)
Great Horned Owl, <i>Bubo virginianus</i>	Craighead and Craighead (1956), Dunning (1993), Holt (1996), Houston et al. (1998)
Marsh Wren, <i>Cistothorus palustris</i>	Verner (1965, 1971, 1975), Kale (1975), Kroodsmas and Verner (1997)
Mourning Dove, <i>Zenaida macroura</i>	Sayre et al. (1980, 1993), Losito et al. (1990), Losito and Mirarchi (1991), Dunning (1993), Reeves et al. (1993), Sayre and Silvy (1993), Mirarchi and Baskett (1994)
Northern Goshawk, <i>Accipiter gentilis</i>	Haukioja and Haukioja (1970), Henny et al. (1985), Palmer (1988), Hargis et al. (1994), Kennedy et al. (1994), Reynolds et al. (1994), Squires and Reynolds (1997)
Northern Spotted Owl, <i>Strix occidentalis caurina</i>	Carey et al. (1989), Franklin et al. (1990), Guitierrez et al. (1995), Burnham et al. (1996)
Pileated Woodpecker, <i>Dryocopus pileatus</i>	Bull (1987), Bull and Meslow (1988), Mellen et al. (1992), Bull and Jackson (1995)
Raccoon, <i>Procyon lotor</i>	Cowan (1973), Fritzel (1978), Fiero and Verts (1986), Verts and Carraway (1998), Gehrt and Fritzel (1999)
Red fox, <i>Vulpes vulpes</i>	Livezey and Evendon (1943), Scott (1943), Wilcomb (1948), Storm (1965), Sargent (1972), Storm et al. (1976), Voight (1987), Verts and Carraway (1998)
Red-tailed Hawk, <i>Buteo jamaicensis</i>	Craighead and Craighead (1956), Luttich et al. (1971), Seidensticker and Reynolds (1971), Henny and Wight (1972), Johnson (1975), Peterson (1979)
Western Meadowlark, <i>Sturnella neglecta</i>	Kendeigh (1941), Lanyon (1957, 1994), Dunning (1993)

was set to ensure that population size estimates were free from the influence of transient behaviors resulting from the model's initial conditions. That is, for each species, we set the number of simulation years to a value that ensured the population would achieve a steady state in each of the five landscapes. This steady-state population size was the value that was ultimately recorded for each species-landscape combination. Simulations were always initiated with every breeding site occupied by an adult, which ensured that each population had the best possible chance to establish itself throughout the landscape.

The first step in running a PATCH simulation involves breaking a landscape up into territory-sized units. This process is accomplished by merging the GIS data with an array of hexagonal cells. The hexagon size is set to the size of a typical territory for an individual of the species being modeled. When the territory-allocation process is finished, each individual hexagon has a score, which is equal to the arithmetic average of the species-habitat preferences associated with each of the data pixels contained within it. A minimum threshold quality for breeding can be established using an estimate of a species' minimum territory size. But in these simulations, individuals were allowed to settle

and reproduce in every hexagon with a nonzero score (although poor quality sites tended to be passed over in favor of better ones). A maximum territory size can also be specified, and this value is used in poor quality regions of a landscape to assemble breeding territories from parts of multiple hexagons. This feature has no effect if all hexagons with habitat are made suitable for breeding.

Movement in PATCH is the process through which individuals locate and claim unoccupied breeding sites. Available movement strategies include a random walk and an "intelligent" search, in which an individual is allowed to move directly to the best available breeding site within its search radius. All but one of the 17 species modeled with PATCH utilized a variety of patchily distributed habitats. The exception, the marsh wren, is restricted during the breeding season to the vegetation immediately adjacent to wetlands, lakes, and reservoirs. For this reason, and for lack of data suggesting otherwise, we used a random walk as the movement strategy for every species except the marsh wren, which used the intelligent search option. PATCH allows the user to bias its random walks towards good habitat, and we used the model's default level of bias in these simulations. The result was that diffusion rates

TABLE 3. The parameter values used to conduct PATCH simulations for the 17 wildlife species examined.

Species	Territory size (ha)		Movement ability		Fecundity		Survival			Vital-rates factor		Lambda if hexagon score is 5.0
	Actual	PATCH	Distance (km)	Steps	Stage 1	Stage 2	Stage 0	Stage 1	Stage 2	Initial Final		
										Initial	Final	
Black-capped Chickadee	3.7	3.24	11.20	58	2.340		0.394	0.394		65	35	1.50
Blue Grouse	2.1	2.02	2.00	13	1.910		0.400	0.560		69	69	1.00
Bobcat	4235.0	4196.88	56.00	8	1.400		0.689	0.689		100	100	1.00
Cooper's Hawk	59.0	60.48	79.00	95	1.050		0.250	0.650		44	44	1.00
Coyote	460.0	451.44	154.00	67	2.800		0.290	0.610		77	58	1.15
Douglas squirrel	0.7	0.81	0.32	4	0.750		0.200	0.600		34	34	1.00
Gray Jay	80.2	77.76	11.00	12	0.900		0.315	0.820		58	58	1.00
Great Horned Owl	210.0	210.60	75.00	48	0.350	0.350	0.680	0.760	0.850	55	47	1.10
Marsh Wren	1.0	1.08	4.10	37	1.740		0.121	0.330		27	20	1.30
Mourning Dove	0.8	0.81	17.80	184	1.800		0.350	0.520		58	49	1.10
Northern Goshawk	170.0	161.46	100.00	74	0.550	1.150	0.330	0.660	0.810	57	57	1.00
Northern Spotted Owl	332.0	338.58	98.00	50	0.205	0.340	0.260	0.844	0.844	47	47	1.00
Pileated Woodpecker	220.0	210.60	8.70	6	1.130		0.640	0.640		74	74	1.00
Raccoon	150.0	136.08	16.00	13	0.720	0.930	0.770	0.720	0.840	98	98	1.00
Red fox	650.0	631.80	108.00	40	1.490		0.480	0.480		60	42	1.25
Red-tailed Hawk	233.0	210.60	184.00	118	0.685		0.460	0.800		59	49	1.10
Western Meadowlark	8.5	6.08	1.60	6	1.220		0.160	0.530		34	24	1.30

Notes: When data permitted, a three-stage-class Leslie matrix was developed. Otherwise, a two-stage model was used, and the stage 2 survival and fecundity values were left blank. The vital-rates factor was initially set so hexagons with a score of 5.0 would be assigned a projection matrix with a lambda value of 1.0. Both this initial value and the value ultimately used in a simulation (see *Methods*) are shown. The rightmost column contains the lambda values corresponding to a hexagon score of 5.0 and the final vital rates factor.

were slightly higher than with a true random walk (Schumaker 1998), and that individuals gravitated somewhat towards clusters of good habitat.

Survival and reproductive rates are supplied to PATCH as a population projection matrix. The user must also associate this matrix with a specific hexagon score and select interpolation functions that allow PATCH to assign new matrices to hexagons with different scores. Typically, hexagons with higher scores are assigned better matrices (larger survival and reproductive rates) and those with lower scores receive poorer matrices. The survival and reproductive rates actually experienced by an individual are thus a function of the values supplied to the model's interface, the quality of the habitat presently occupied (which can change at each time step), and the interpolation scheme selected by the user. Once a hexagon is assigned a projection matrix, it can also be assigned a lambda-value. Lambda, a matrices' dominant eigenvalue (Caswell 1989, Gotelli 1995), determines whether a site can be expected to function as a demographic sink or source.

PATCH's "convex" interpolation function (a cubic function reflected about the one-to-one line) was used to assign survival rates to hexagons, based upon their scores, while the linear interpolation function was used with fecundity. These selections were made because together they reflect the principle that energy will be devoted primarily to survival, and secondarily to re-

production. In addition, this combination of interpolation functions allowed the "vital-rates factor" parameter to be set at its target value for the largest number of species. All of PATCH's interpolation functions have a y-intercept of zero, and the result of this parameterization was that, in a hexagon with a score of δ ,

$$S(\delta) = S_{\max} \left[1 - \left(1 - \frac{\delta}{\delta_{\max}} \right)^3 \right] \tag{1}$$

$$F(\delta) = F_{\max} \left(\frac{\delta}{\delta_{\max}} \right) \tag{2}$$

where $S(\delta)$ and $F(\delta)$ refer to the survival and fecundity values experienced by an individual occupying the site. δ_{\max} is the largest possible hexagon score, which was always 10 in these simulations because that was the score of a hexagon composed strictly of the best habitat. S_{\max} and F_{\max} are the survival and reproductive rates that would be assigned in a hexagon with a score of δ_{\max} . PATCH computes S_{\max} and F_{\max} from the input survival and fecundity values and a user-supplied specification for what habitat quality these parameters are to be associated with. For example, if the juvenile survival rate for a species was 0.500, and the user stipulated that this was to be assigned to habitat that was 60% of the optimal habitat quality (which here is scored 10), then from Eq. (1), S_{\max} would be computed from the following relationship:

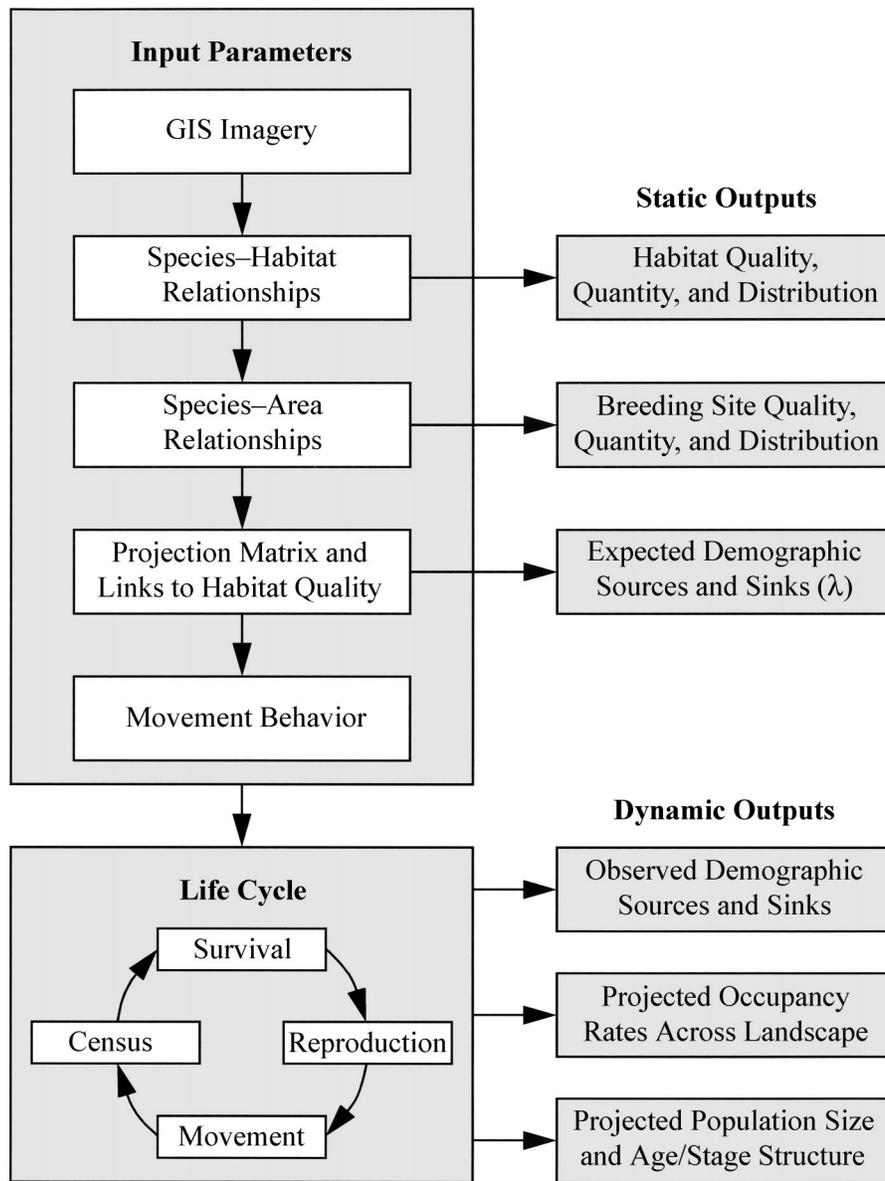


FIG. 1. The PATCH model's structure and data needs are collected within the two boxes on the left. Static and dynamic model outputs are displayed along the right (static outputs can be obtained without running a simulation). Increasingly sophisticated analyses become possible with each successive input parameter. Our simple habitat-based assessments correspond to the top-most output. Our complex individual-based assessments are characterized by occupancy rates and population sizes.

$$S_{\max} = \frac{0.500}{\left[1 - \left(1 - \frac{0.6 \times 10}{10}\right)^3\right]} = 0.534. \quad (3)$$

To associate the input survival and fecundity values with a particular habitat quality, the "vital-rates factor" parameter was set to a percentage of the best possible hexagon score. The example of Eq. (3) would correspond to a vital-rates factor of 0.6. The simulations reported here were conducted with vital-rates factors selected so that hexagons with a score of 5.0 would be

assigned a Leslie matrix with a dominant eigenvalue of 1.0. This corresponded to a convention adopted by the expert panels that developed our species-habitat relationships. These panels stipulated that habitats of score 5 would represent the dividing point between demographic sinks and sources. In eight cases, a population known to be extant could not persist in the landscape with the vital-rates factor obtained this way. In these cases, the vital-rates factor was lowered until the population stabilized, but not so low that a significant number of floaters appeared on the landscape. It

was generally assumed that large accumulations of floaters—adult individuals unable to locate breeding sites—were unrealistic and such situations were taken as an indication that the vital-rates factor was set too low.

Table 3 summarizes the input parameters for the 17 wildlife species examined using the PATCH model. Because it uses raster GIS data, PATCH cannot construct territories of any arbitrary size. The column in Table 3 labeled “PATCH territory size” contains the actual territory sizes used in the simulations, which were set as close to the literature-based estimate as possible. PATCH’s maximum movement distance parameter is specified as a number of steps from a hexagon to one of its six neighbors, and movement ability is thus reported in both kilometers and the equivalent number of steps. The “stage 2 fecundity” and “stage 2 survival” values in Table 3 were left blank if rates for a distinct subadult stage could not be found in the literature. Our stage 0 fecundity estimates were always zero. The vital-rates factor values in Table 3 determine the lambda value associated with a hexagon of a particular score. We initially set the vital-rates factor so that hexagons with a score of 5.0 corresponded to a lambda value of 1.0. But the final vital-rates factor used in a simulation sometimes had to be set lower than this initial value. Both the initial and final vital-rates factors are provided in Table 3. The right-most column of Table 3 shows the lambda values (obtained using the final vital-rates factor) associated with hexagons having a score of 5.0.

RESULTS

Changes in wildlife habitat

Relative to Circa 1990, habitat for all groups of species changed more in the Historic landscape than in any of the alternative future landscapes (Fig. 2). For each of the alternative future landscapes, the median percentage change for each of the native vertebrate groups, as well as for all native species taken together, was less than $\pm 6\%$. In contrast, the median percentage change in habitat in the Historic landscape relative to Circa 1990, for all groups of species except introduced, was at least $+20\%$. Median percentage change in habitat for introduced species in the alternative future landscapes was $+10\%$ to $+33\%$, but declined -50% in the Historic landscape. The median percentage change in habitat for native reptile species was positive in all future landscapes (Fig. 2). In part, this was because of a greater amount of young-age conifer forest in the uplands in Plan Trend 2050 and Development 2050, and greater amount of open habitat in the valley in Conservation 2050, both important for reptiles. The $+52\%$ change in reptile habitat in the Historic landscape relative to Circa 1990 was associated with greater amounts of open habitat such as oak savanna, dry shrub, and natural grass. Our results were more dra-

matic for the percentage of species with increasing or decreasing habitat. The Historic and Conservation 2050 scenarios had, respectively, 44% and 31% greater numbers of species with increased habitat than with decreased habitat, relative to 1990. In contrast, Plan Trend and Development had more species (10% and 39%, respectively) with decreased habitat than with increased habitat.

Changes in population size

PATCH simulations were conducted for 17 of the 279 wildlife species found in the basin. These simulations generated a number of measures of population performance for each species and landscape (Fig. 1), but the focus here is on the size of the breeding population. PATCH is a females-only model, and its census is conducted after the young-of-the-year have dispersed in search of breeding sites. Therefore, the number of breeders in a population is roughly equivalent to one-half of the number of individuals. The lack of environmental stochasticity in these simulations makes our results optimistic. Assuming environmental stochasticity was included by drawing vital rates from symmetric distributions centered on the values shown in Table 3, the effect would be to decrease the mean time to extinction, and lower the overall population sizes.

Fig. 3 displays the principal results from the PATCH simulations, expressed as a changes in mean habitat quality and in breeder population size, both relative to Circa 1990 conditions. For each species, mean habitat quality was computed as the sum of habitat weights assigned to each pixel in the landscape (nonhabitat and areas outside a species’ range were weighted zero), divided by the total number of pixels in the image. All 17 simulated wildlife species had larger populations under the Historic landscape than in Circa 1990, with seven increasing by $>50\%$. This strong response can be attributed to the Historic landscape’s low level of habitat fragmentation and its relative abundance of habitat for most species (Fig. 3). While populations tended to be larger (14 of 17 species) under Conservation 2050 than in Circa 1990, they were usually smaller than under the Historic scenario. Twelve species experienced an increase in mean habitat quality in the transition from Circa 1990 to Conservation 2050 conditions. Ten species increased $>10\%$ (relative to Circa 1990) under Conservation 2050, compared to three under Plan Trend 2050 and one under Development 2050. Four species increased $>25\%$ under Conservation 2050. Just one species declined by more than 10% under Conservation 2050, compared to five and nine under Plan Trend 2050 and Development 2050, respectively. The transition from Circa 1990 to Development 2050 caused four species to decline by $>25\%$, and one to drop by $>50\%$.

Fig. 4 shows estimated changes in simulated occupancy rates, for four of the 17 species, resulting from

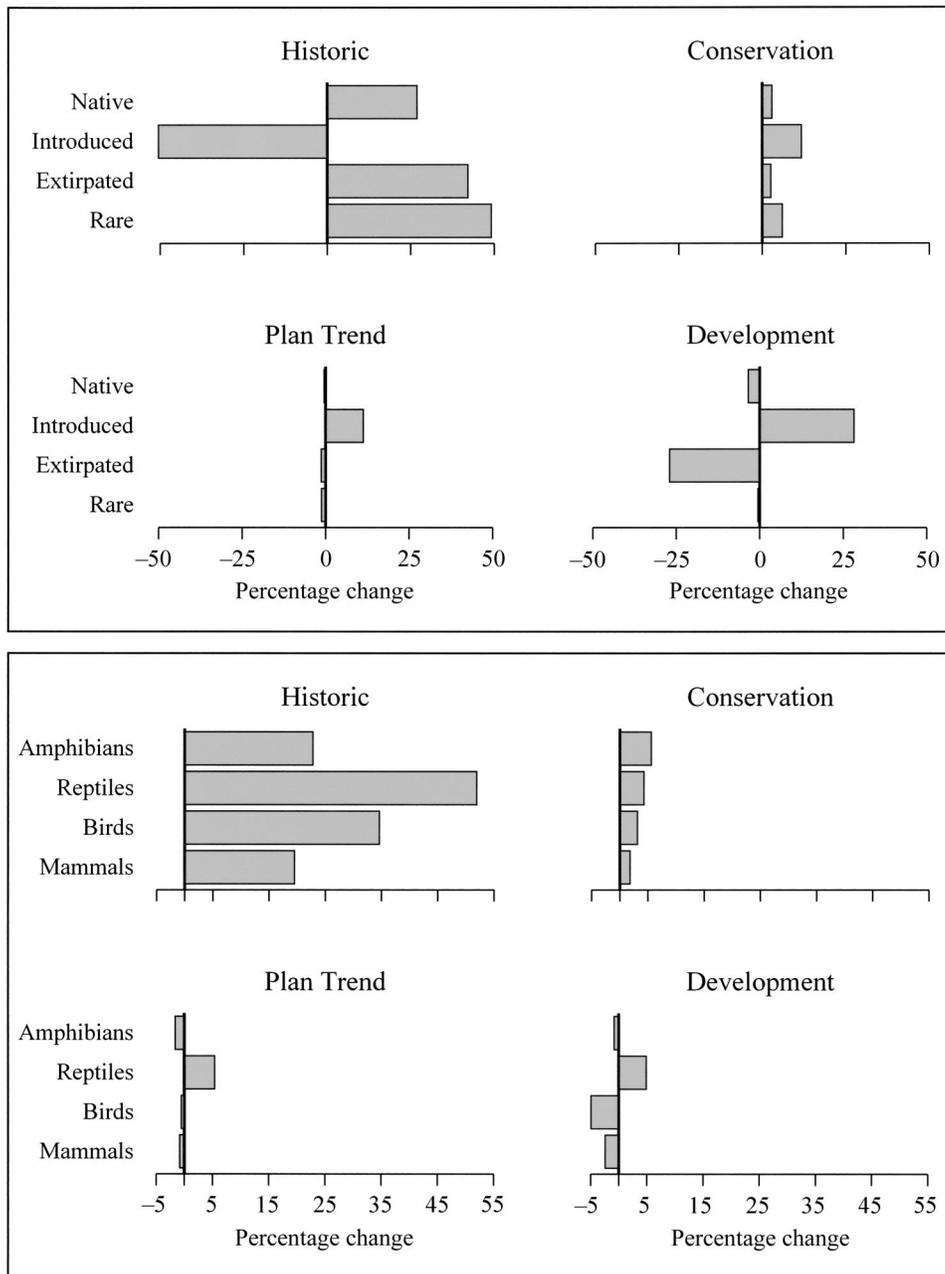


FIG. 2. Percentage change in habitat, by scenario, for native, introduced, extirpated, and rare species (top) and four taxonomic groups of species (bottom), as compared to Circa 1990.

the transition from Circa 1990 to the Historic and three alternative future conditions. Occupancy rates were calculated after a population had reached a steady state, by tallying the number of times each hexagon was occupied by a breeder (as opposed to a floater), and summing this quantity across every replicate simulation. The blue grouse's small territory size coupled with its dependence on older conifers caused it to track fine-scale patterns of forest harvesting. Thus, this species

exhibits intricate patterns of loss and gain, with good areas closely interspersed among bad ones. The red fox, by comparison, has a much larger territory size and is more of a generalist than the Blue Grouse. But the fox's principal habitats (forest and grasslands) are heavily managed, and while it consequently displays a mixture of losses and gains, the spatial patterns associated with these transitions are simpler than those of the Blue Grouse. The Northern Spotted Owl populations were

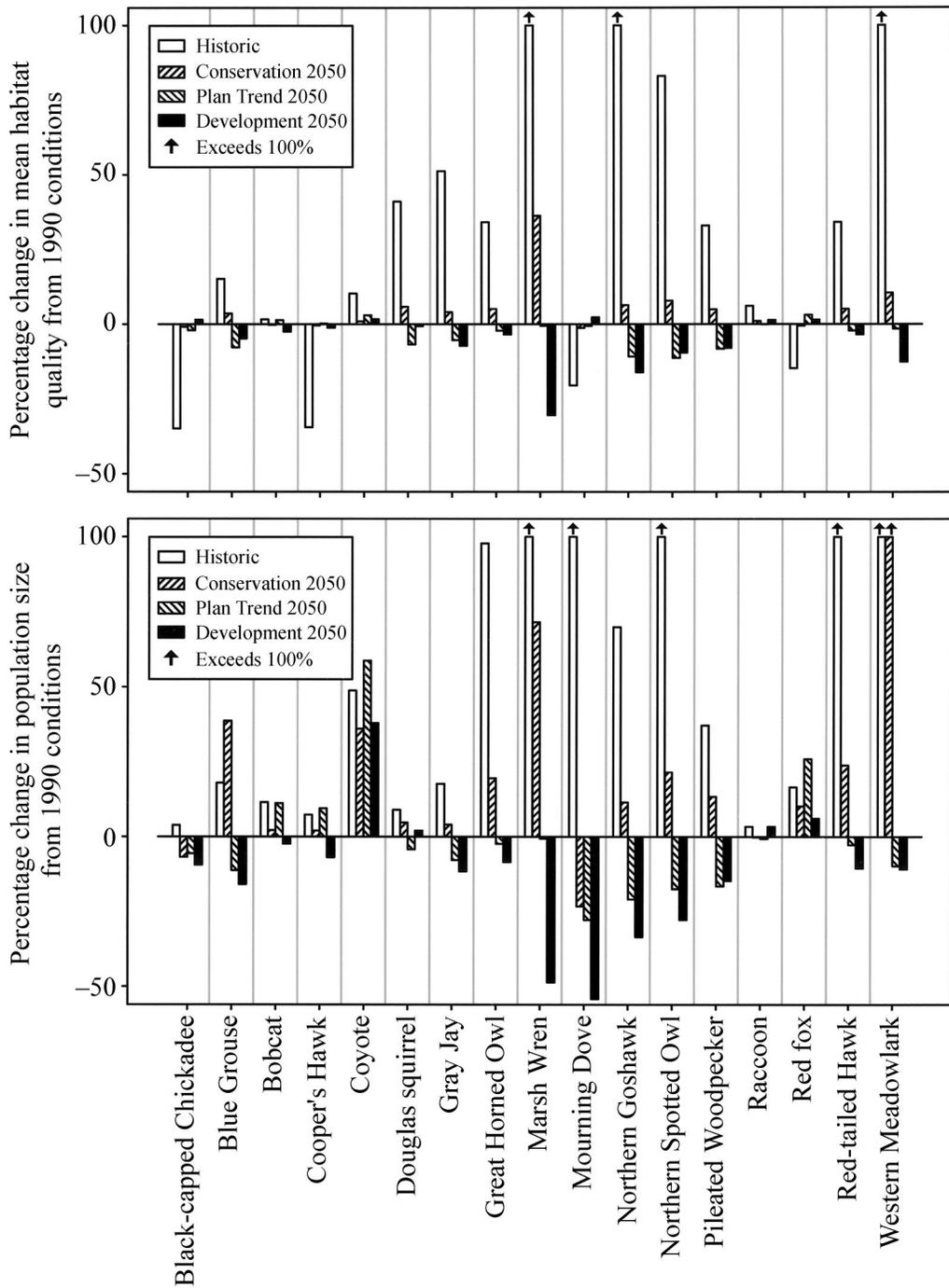


FIG. 3. The percentage change in mean habitat quality (top), and in breeding population size (bottom), from that estimated under Circa 1990 conditions. In several cases the change exceeded 100%. These values were truncated and marked with an arrow.

much larger under the Historic conditions than Circa 1990, improved under Conservation 2050, and declined under Plan Trend 2050 and Development 2050. A projected increase of the Northern Spotted Owl population was dramatic in the Cascade foothills and coast range

under the Historic conditions. Areas of loss and gain under the alternative future conditions were concentrated in the Cascade mountains, and were buffered to a degree by the influence of the Northwest Forest Plan (Forest Ecosystem Management Assessment Team

1993) on these scenarios. In contrast, the coyote, a supreme generalist, did considerably better under the Historic conditions and all three alternative futures. The coyote did the best under the Plan Trend 2050 conditions, where the interface between grasslands, open forests, and low-density urban areas was at a maximum. The principal areas of expansion for the coyote populations appeared to be the lowland forests, and portions of the valley bottom under Historic conditions.

Model comparisons

Our model comparisons were constructed using the mean habitat-quality estimates from the habitat-based assessment and the population sizes produced by PATCH. Fig. 5 displays the principal results of the comparison. Data points corresponding to a single species are connected by a line, in order of mean habitat quality, and the populations are separated into two functional groups (note the number of individuals has sometimes been reduced by a fraction). Mean habitat quality for a species was computed as the sum of habitat weights assigned to each pixel in the landscape divided by the total number of pixels in the image. Pixels of nonhabitat, and those falling outside a species' range, were weighted zero. The upper panel in Fig. 5 displays the nine species for which our simple habitat-based assessment and our complex SEPM appear closely, and positively, correlated. The bottom panel contains eight species for which the correlation between the assessments was weak or negative. This analysis suggests that, for roughly half of these species, a simple measure of habitat quality might be developed that reliably predicts the number of individuals. For the remaining organisms, the details of habitat pattern may have a profound influence on population dynamics, and thus our habitat-based analysis might simply be insufficient in these cases. Alternatively, our weak fits could be explained by errors in the design or parameterization of our SEPM.

Fig. 6 shows the percentage change in population size, from Circa 1990 conditions, plotted as a function of the percentage change in mean habitat quality. Fig. 6 has a logarithmic vertical axis, and the one-to-one line (shown as the solid line in the figure) thus appears nonlinear. Small gains in habitat quality were frequently associated with large increases in projected population size, as illustrated by the western meadowlark under the transition from Circa 1990 to Conservation 2050. In a few cases, an increase in mean habitat quality was accompanied by a decrease in population size, as in the mourning dove's response to the shift from Circa 1990 to Development 2050. Such counterintuitive results could be explained by the sensitivity of our complex model to amounts and patterns of habitat fragmentation. In some cases, the modeled population size responded dramatically to landscape change. For example, the transition from Circa 1990 to Historic con-

ditions was accompanied by a more than 300-fold increase in the Western Meadowlark population. While many of the data points in Fig. 6 fall remarkably close to the one-to-one line, the trend is for percentage change in habitat quality to underestimate the percentage change in population size. That is, most of the points in Fig. 6 fall above the positive segment, or below the negative segment, of the one-to-one line.

The conclusions we drew from our simple model, about the responses of species groups to landscape change, were based on the assumption that errors inherent in using habitat as a surrogate for population viability average out across a large array of species. Our model comparisons shed some light on this assumption, particularly as displayed in Fig. 6. Percentage change in mean habitat quality consistently underestimated percentage change in breeding population size. This indicates that errors in our habitat-based assessment may tend to average out when the groups of species examined include some experiencing habitat gains and others experiencing losses. Extrapolating from this conclusion (which assumes a fair degree of confidence in our SEPM), it follows that our habitat-based analysis of the consequences for biodiversity of a shift from Circa 1990 to Plan Trend 2050 or Development 2050 conditions may be more accurate than the analogous conclusions drawn for the Historic or Conservation 2050 conditions. The former two transitions were accompanied by a mixture of habitat losses and gains, both across species groups and taxa, while the latter two transitions saw habitat conditions generally improve.

CONCLUSIONS

In terms of overall suitability for wildlife, our two models produced identical rankings for the five WRB maps. Not surprisingly, the Historic landscape was the best overall in terms of both habitat quality and size of the simulated wildlife populations. The one exception to this rule involved the introduced species, for whom the Historic landscape constituted a considerable decrease in habitat quality. The Conservation 2050 alternative future was ranked second by both of our analyses, followed by Circa 1990, Plan Trend 2050, and finally Development 2050. Changes in habitat quality and population size observed in transitions between Circa 1990 and the three alternative futures were typically small compared to changes observed in the transition to Historic conditions. All 17 simulated wildlife populations did better under the Historic conditions than Circa 1990, even though some experienced lower values of mean habitat quality. Most of the 17 species did more poorly under the Development 2050 conditions than under Circa 1990, and the percentage loss in projected population size tended to exceed the percentage loss in habitat quality. Our three alternative future landscapes were all constrained by the North-

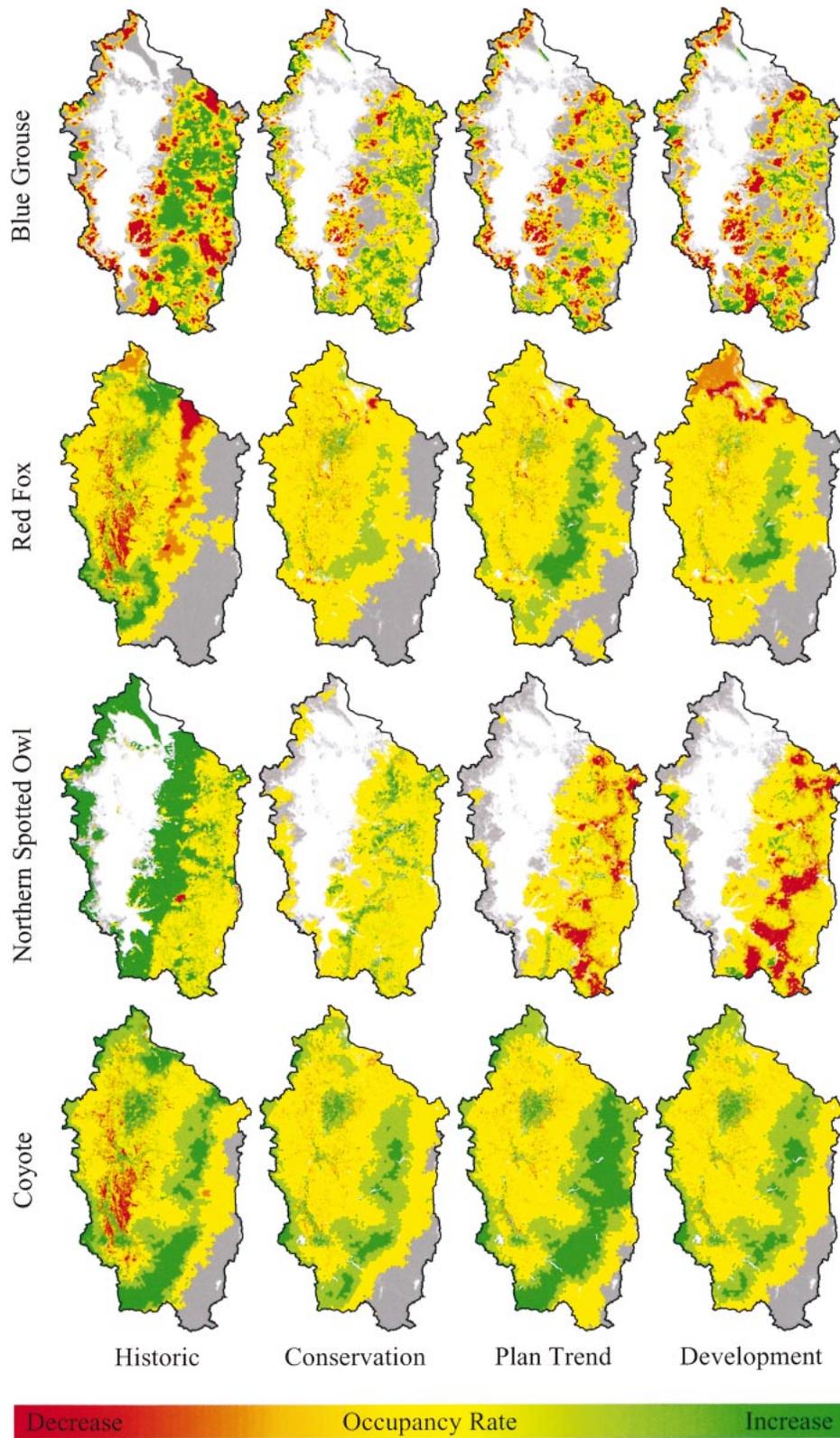


FIG. 4. The change in habitat occupancy rates from those of Circa 1990, for four species. Red areas indicate a decrease in occupancy. Yellow represents little or no change, and rates increased in the green regions. The maps being compared to Circa 1990 are indicated along the bottom. White and gray depict nonhabitat and unused habitats, respectively.

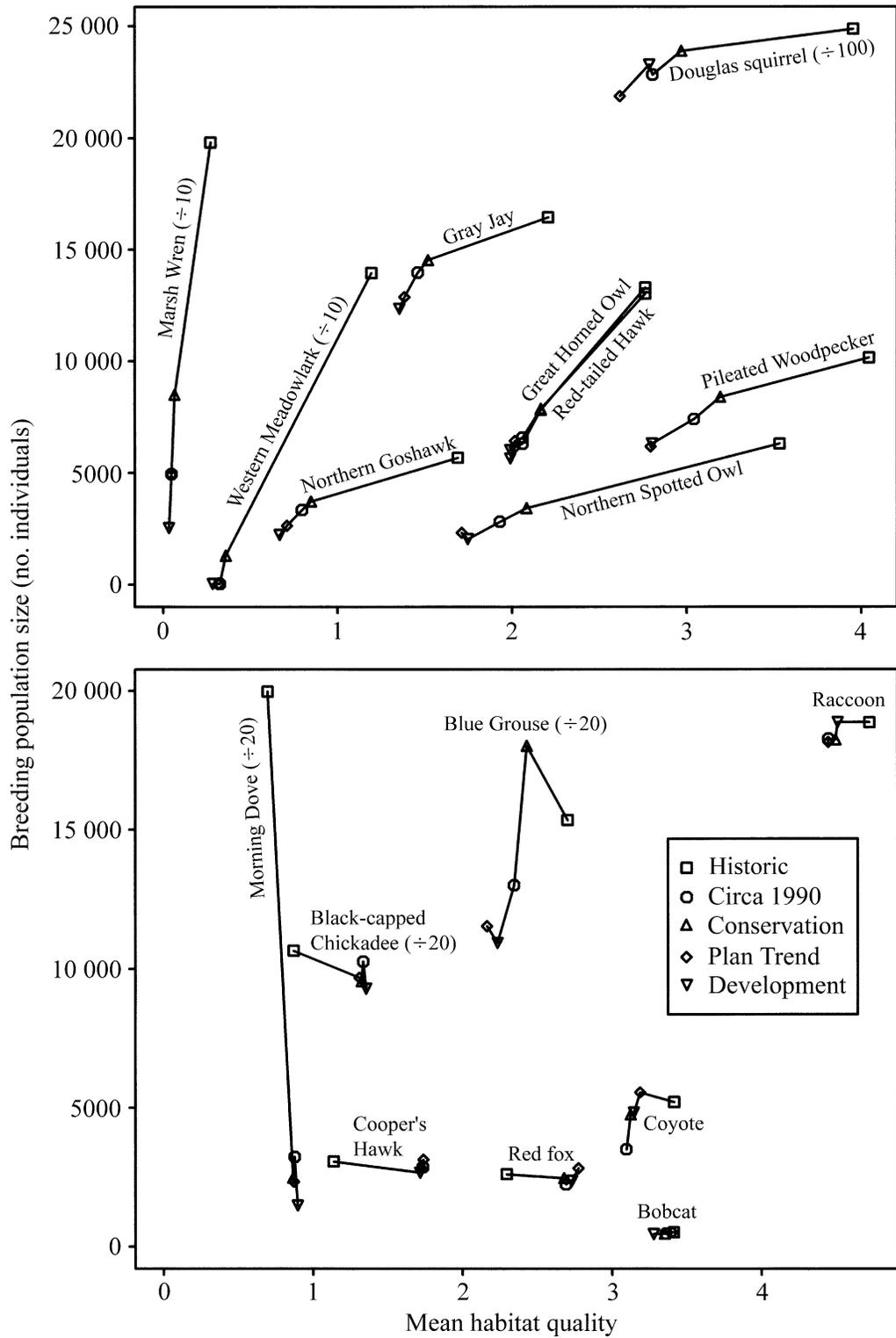


FIG. 5. The relationship between mean habitat quality (obtained from our simple habitat-based assessment) and population size (derived from our complex individual-based model). The correlations were good for the nine species in the upper graph, and poor for the eight in the lower one. Some of the population sizes were rescaled to limit the range of the vertical axes. In these cases, the population size was divided by the value indicated in parentheses next to the species name. For example, our simulated Douglas squirrel breeding population sizes were actually 100 times larger than the values indicated in the figure.

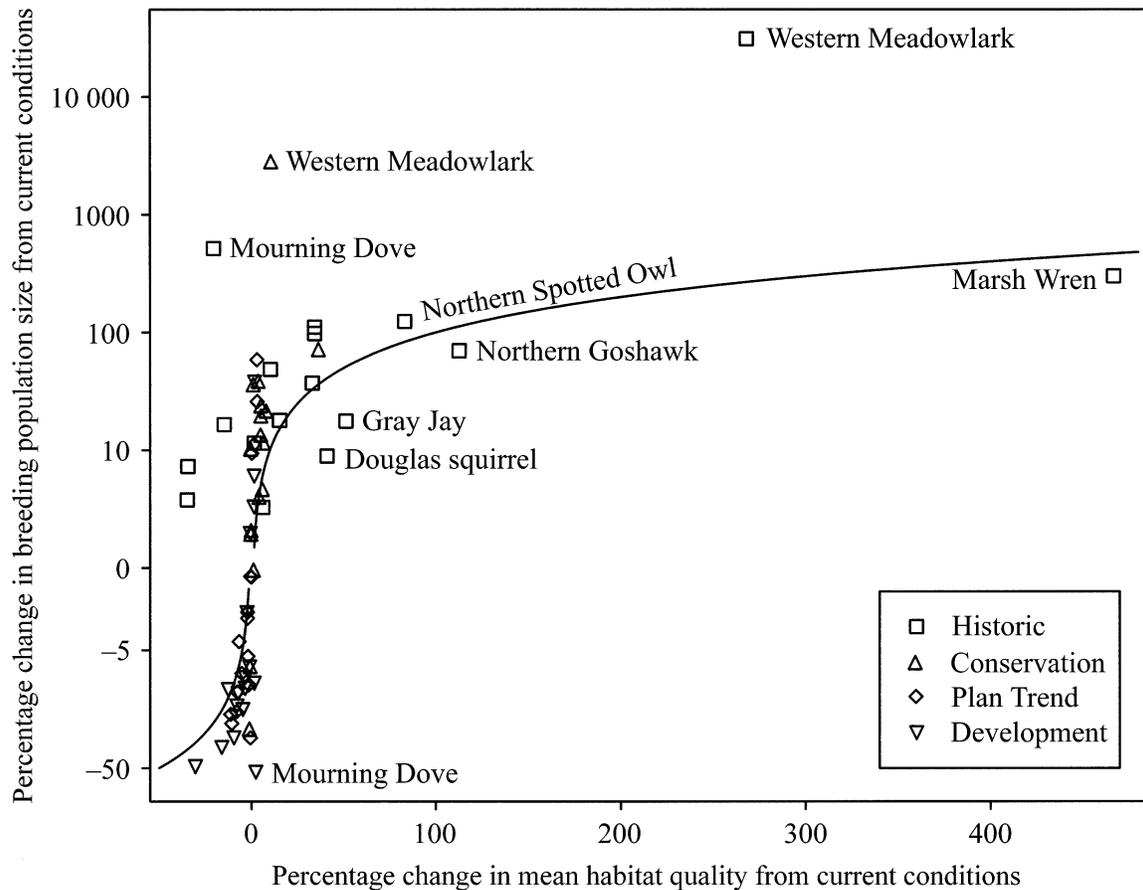


FIG. 6. The relationship between changes in mean habitat quality, relative to Circa 1990 conditions, and the corresponding changes in breeding population size. The solid line displays the path along which the x- and y-axis values are identical. Species labels were included when it was possible to do so legibly.

west Forest Plan (Forest Ecosystem Management Assessment Team 1993), and for several species (e.g., the Northern Spotted Owl), population response can be explained to a large extent by this commonality.

The results from our two different assessments were well correlated for about half of the species examined using PATCH. In these cases, an expression of the form population size = slope × mean habitat quality + intercept may be adequate to explain much of the variance associated with the model predictions. For the remaining species, the details of landscape pattern would have to be considered to anticipate the population responses to landscape change. Because the 17 species were selected on the basis of life history data availability, rather than as representative of well-defined groups of species or as a probability sample, it is difficult to generalize from these results. We did not develop a working hypothesis explaining when our two assessments should disagree. Instead, we simply observe that such discrepancies all involved habitat generalists, and that they would have been less pronounced if the Historic landscape had been left out of the anal-

ysis. It would be instructive to include models of intermediate complexity, such as incident-function models (Hanski 1994, Moilanen and Hanski 1998), in future analyses.

It may seem disconcerting that a large number of the simulated populations responded negatively to increases in mean habitat quality. Yet there are a number of mechanisms that could cause this behavior. For instance, it is easy to imagine improving a landscape's overall habitat quality in such a way that, when examined at the scale of individual territories, demographic sources become sinks but sinks are not converted to sources. Similarly, adding good habitat far from a wildlife population center might do little to benefit a species, while lowering the habitat quality within or adjacent to a population center could do significant harm. In addition, our strategy for running the individual-based model often involved conducting simulations for large numbers of years. This allowed small shifts in population growth rates to grow into large changes in overall population size. Given the differences in complexity between our simple and complex

assessments (Fig. 1), it may be more remarkable when the models exhibit good correlations than when they appear at odds.

The implications of our work for land use planning in the Willamette River Basin are in part straightforward and in part ambiguous. Our work suggests the land use policies captured in the Conservation 2050 future scenario will benefit a majority of the wildlife species native to the WRB. While these changes would not restore most populations to their Pre-European settlement levels, they would be largely positive and significant. We also conclude that, overall, the Plan Trend 2050 and Development 2050 scenarios are similar and generally negative in their consequences for wildlife, with the former being less damaging than the latter. Our work supports the notion that wildlife populations can respond in very different ways to incremental changes in habitat quantity, quality, and pattern. Some populations will expand or contract in proportion to habitat changes. Some populations will appear buffered against habitat loss or gain (up to a point), while still others will respond to small landscape changes with large shifts in population size. If a goal of management is to conserve viable populations of all extant wildlife species, then it is unlikely that a simple methodology could be developed to help planners safely mix and match attributes of the three future scenarios. The best process for guiding development might instead involve breaking species into screening classes. For some species, habitat quality and quantity could probably be used as a surrogate for population size. For others, more detailed analyses would have to be performed. Difficult cases might be grouped into response classes and each examined using a single "indicator" species. While still cumbersome, such a tiered approach would be very efficient relative to an exhaustive species-by-species analysis.

From a management perspective, these results are both encouraging and discouraging. Assuming our models are roughly accurate, this study lends credibility to the notion that "coarse filter" screening tools might be developed to quickly assess the consequences for wildlife of management actions such as those embodied in our three alternative futures. On the other hand, our results suggest that such simple tools will often fail dramatically. This study cannot, in its present form, identify general rules for predicting wildlife responses to landscape change. To reach this goal would require extensive model validation and sensitivity analysis, and study of a broader array of species than those we examined here using PATCH. The effort required to construct, parameterize, and validate SEPMs can make an investigator anxious to embrace their predictions. But the greatest contribution of studies such as this may not lie in the development of more sophisticated analytic tools, but instead in the identification of

species-landscape combinations where our simplest models work the best.

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LITERATURE CITED

- Andrews, H. J., and R. W. Cowlin. 1940. Forest resources of the Douglas-fir region. Miscellaneous Publication 389. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Armleder, H. M. 1980. Habitat use and movements of hens and broods in relation to the demography of Blue Grouse. Thesis. University of Toronto, Toronto, Ontario, Canada.
- Bailey, T. N. 1974. Social organization in a bobcat population. *Journal of Wildlife Management* **38**:435-446.
- Baker, J. P., D. W. Hulse, S. V. Gregory, D. White, J. Van Sickle, P. A. Berger, D. Dole, and N. H. Schumaker. 2004. Alternative futures for the Willamette river basin. *Ecological Applications* **14**:313-324.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**: 821-841.
- Bekoff, M. 1977. *Canis latrans*. *Mammalian Species* **79**:1-9.
- Bigger, D., and D. Vesely. 2000. Life history database for vertebrates of the Willamette river basin. Final Project Report to U.S. Environmental Protection Agency. Pacific Wildlife Research, Inc., Corvallis, Oregon, USA.
- Boag, D. A. 1966. Population attributes of Blue Grouse in southwestern Alberta. *Canadian Journal of Zoology* **44**: 799-814.
- Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* **11**:406-421.
- Bolsinger, C. L., and K. L. Waddell. 1993. Area of old-growth forests in California, Oregon, and Washington. Resource Bulletin PNW 57. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Booth, D. E. 1991. Estimating prelogging, old-growth in the Pacific Northwest. *Journal of Forestry* **89**:25-29.
- Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. *Canadian Journal of Anthropology* **5**:65-86.
- Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. *Auk* **80**:9-47.
- Brewer, R. 1978. Winter home ranges of Black-capped Chickadees in southern Michigan oak forest. *Jack-Pine Warbler* **56**:96-98.
- Brooker, L., M. Brooker, and P. Cale. 1999. Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use, and dispersal mortality. *Conservation Ecology* **3**(4). [Online: (<http://www.consecol.org/vol3/iss1/art4>).]
- Bull, E. L. 1987. Ecology of the Pileated Woodpecker in northeastern Oregon. *Journal of Wildlife Management* **51**: 472-481.
- Bull, E. L., and J. E. Jackson. 1995. Pileated Woodpecker (*Dryocopus pileatus*). In A. Poole and F. Gill, editors. *The birds of North America*, No. 148. The Academy of Natural

- Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Bull, E. L., and E. C. Meslow. 1988. Breeding biology of the Pileated Woodpecker—management implications. Research Note **PNW-RN-474**. U.S. Department of Agriculture, Forest Service, Portland Oregon, USA.
- Burke, D. M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* **10**:1749–1761.
- Burnham, K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. Pages 92–101 in E. D. Forsman, S. DeStefano, M. G. Raphael, and R. J. Gutierrez, editors. *Demography of the Northern Spotted Owl*. Studies in Avian Biology, No. 17. Cooper Ornithological Society, Lawrence, Kansas, USA.
- Carey, A. B., S. P. Horton, and J. A. Reid. 1989. Optimal sampling for radio telemetry studies of spotted owl habitat and home range. U.S. Forest Service, Pacific Northwest Research Station Research Paper **PNW-RP-16**.
- Caswell, H. 1989. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.
- Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* **2**:387–396.
- Clarke, S. E., D. White, and A. L. Schaedel. 1991. Oregon, USA, ecological regions and subregions for water quality management. *Environmental Management* **15**:847–856.
- Cohen, W. B., T. K. Maierperger, T. A. Spies, and D. R. Oetter. 2001. Modeling forest cover attributes as continuous variables in a regional context with Thematic Mapper data. *International Journal of Remote Sensing* **22**:2279–2310.
- Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* **5**:17–19.
- Cowan, W. F. 1973. Ecology and life history of the raccoon (*Procyon lotor hirtus* Nelson and Goldman) in the northern part of its range. Dissertation. University of North Dakota, Grand Forks, North Dakota, USA.
- Craighead, J. J., and F. C. Craighead. 1956. Hawks, owls and wildlife. Dover Publications, New York, New York, USA.
- Doak, D. F. 1995. Source–sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly bear. *Conservation Biology* **9**:1370–1379.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. *Ecology* **75**:615–626.
- Dunning, J. B., Jr. 1993. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida, USA.
- Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**:3–11.
- Edwards, T. C., Jr., E. T. Deshler, D. Foster, and G. C. Moisen. 1996. Adequacy of wildlife habitat relation models for estimating spatial distributions of terrestrial vertebrates. *Conservation Biology* **10**:263–270.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–610.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**:273–292.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Fiero, B. C., and B. J. Verts. 1986. Age-specific reproduction in raccoons in northwestern Oregon. *Journal of Mammalogy* **67**:169–172.
- Foppen, R. P. B., J. P. Chadron, and W. Liefveld. 2000. Understanding the role of sink patches in source–sink metapopulations: Reed Warbler in an agricultural landscape. *Conservation Biology* **14**:1881–1892.
- Forest Ecosystem Management Assessment Team. 1993. Forest Ecosystem Management: an ecological, economic, and social assessment. Joint publication of the U.S. Forest Service, National Marine Fisheries Service, Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, and U.S. Environmental Protection Agency, Washington, D.C., USA.
- Forys, E. A., and S. R. Humphrey. 1999. Use of population viability analysis to evaluate management options for the endangered lower keys marsh rabbit. *Journal of Wildlife Management* **63**:251–260.
- Franklin, A. B., J. P. Ward, R. J. Gutierrez, and G. I. Gould, Jr. 1990. Density of Northern Spotted Owls in Northwest California. *Journal of Wildlife Management* **54**:1–10.
- Fritzell, E. K. 1978. Aspects of raccoon (*Procyon lotor*) social organization. *Canadian Journal of Zoology* **56**:260–271.
- Gehrt, S. D., and E. K. Fritzell. 1999. Survivorship of a non harvested raccoon population in south Texas. *Journal of Wildlife Management* **63**:889–894.
- Glase, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. *Living Bird* **12**:235–267.
- Gotelli, N. J. 1995. A primer of ecology. Sinauer, Sunderland, Massachusetts, USA.
- Gurnel, J. C. 1987. The natural history of squirrels. Facts on File, New York, New York, USA.
- Gutierrez, R. J., A. B. Franklin, and W. S. Lahaye. 1995. Spotted Owl (*Strix occidentalis*). In A. Poole and F. Gill, editors. *The birds of North America*, No. 179. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151–162.
- Hargis, C. D., C. McCarthy, and R. D. Perloff. 1994. Home ranges and habitats of northern goshawks in eastern California. *Studies in Avian Biology* **16**:66–74.
- Haukioja, E., and M. Haukioja. 1970. Mortality rates of Finnish and Swedish Goshawks (*Accipiter gentilis*). *Finnish Game Research* **31**:13–20.
- Henny, C. J., R. A. Olson, and T. L. Fleming. 1985. Breeding chronology, molt, and measurements of accipiter hawks in northeastern Oregon. *Journal of Field Ornithology* **56**:97–112.
- Henny, C. J., and H. M. Wight. 1972. Population ecology and environmental pollution: Red-tailed and Cooper's Hawks. Pages 229–250 in *Population ecology of migratory birds: a symposium*. U.S. Fish and Wildlife Service, U.S. Department of Interior, Washington, D.C., USA.
- Holt, J. B., Jr. 1996. A banding study of Cincinnati area Great Horned Owls. *Journal of Raptor Research* **30**:194–197.
- Houston, C. S., D. G. Smith, and C. Rohner. 1998. Great Horned Owl (*Bubo virginianus*). In A. Poole and F. Gill, editors. *The birds of North America*, No. 372. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Hulse, D. W., A. Branscomb, and S. G. Payne. 2004. Envisioning alternatives: using citizen guidance to map future land and water use. *Ecological Applications* **14**:325–341.
- Jamieson, I. G., and F. C. Zwickel. 1983. Dispersal and site fidelity in Blue Grouse. *Canadian Journal of Zoology* **61**:570–573.
- Johnson, S. J. 1975. Productivity of the Red-tailed Hawk in southwestern Montana. *Auk* **92**:732–736.

- Kale, H. W., II. 1975. Ecology and bioenergetics of the Long-billed Marsh Wren, *Telmatorhynchus palustris griseus* (Brewster) in Georgia salt marshes. Publications of the Nuttall Ornithological Club 5:142.
- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373:299–302.
- Kendeigh, S. C. 1941. Birds of a prairie community. *Condor* 43:165–174.
- Kennedy, P. L., J. M. Ward, G. A. Rinker, and J. A. Gessaman. 1994. Post-fledging areas in Northern Goshawk home ranges. *Studies in Avian Biology* 16:75–82.
- Kennelly, J. J. 1978. Coyote reproduction. In M. Bekoff, editor. *Coyotes, biology, behavior and management*. Academic Press, New York, New York, USA.
- Kluyver, H. N. 1991. Food consumption in relation to habitat in breeding Chickadees. *Auk* 78:532–550.
- Koford, R. R. 1982. Mating system of a territorial squirrel (*Tamiasciurus douglasii*) in California. *Journal of Mammalogy* 63:274–283.
- Kroodsmas, D. E., and J. Verner. 1997. Marsh Wren (*Cistothorus palustris*). In A. Poole and F. Gill, editors. *The birds of North America*, No. 308. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Lanyon, W. E. 1957. The comparative biology of the Meadowlarks (*Sturnella*) in Wisconsin. No. 1. Publications of the Nuttall Ornithological Club, Cambridge, Massachusetts, USA.
- Lanyon, W. E. 1994. Western Meadowlark (*Sturnella neglecta*). In A. Poole and F. Gill, editors. *The birds of North America*, No. 194. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Lariviere, S., and L. R. Walton. 1997. *Lynx rufus*. *Mammalian Species* 563:1–8.
- Larsen, K. W., and S. Boutin. 1994. Movement, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75:214–223.
- Lefkovich, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21:1–18.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 35:183–212.
- Lindenmayer, D. B., and H. P. Possingham. 1996. Ranking conservation and timber management options for Leadbeater's possum in Southeastern Australia. *Conservation Biology* 10:235–251.
- Livezey, R., and P. Evendon. 1943. Notes on the western red fox. *Journal of Mammalogy* 24:500–501.
- Losito, M. P., and R. E. Mirarchi. 1991. Summertime habitat use and movements of hatching-year Mourning Doves in northern Alabama. *Journal of Wildlife Management*, 55:137–146.
- Losito, M. P., R. E. Mirarchi, and G. A. Baldassarre. 1990. Summertime activity budgets of hatching-year mourning doves. *Auk* 107:18–24.
- Luttich, S. N., L. B. Keith, and J. D. Stephenson. 1971. Population dynamics of the red-tailed hawk (*Buteo jamaicensis*) at Rochester, Alberta. *Auk* 88:75–87.
- McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65:235–260.
- McNicholl, M. K. 1978. Behavior and social organization in a population of blue grouse on Vancouver Island. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Mellen, T. K., E. C. Meslow, and R. W. Mannan. 1992. Summertime home range and habitat use of pileated woodpeckers in western Oregon. *Journal of Wildlife Management* 56:96–103.
- Mirarchi, R. E., and T. S. Baskett. 1994. Mourning Dove (*Zenaidura macroura*). In A. Poole and F. Gill, editors. *The birds of North America*, No. 117. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. *Ecology* 80:1031–1043.
- Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79:2503–2515.
- Mooij, W. M., and D. L. DeAngelis. 1999. Error propagation in spatially explicit population models: a reassessment. *Conservation Biology* 13:930–933.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. *Wildlife-habitat relationships. Concepts and applications*. The University of Wisconsin Press, Madison, Wisconsin, USA.
- Murphy, M. T. 2001. Source-sink dynamics of a declining Eastern Kingbird population and the value of sink habitats. *Conservation Biology* 15:737–748.
- Nellis, C. H., and L. B. Keith. 1976. Population dynamics of coyotes in Central Alberta, 1964–1968. *Journal of Wildlife Management* 40:389–399.
- Nickell, W. P. 1956. Nesting of the Black-capped Chickadee in the southern peninsula of Michigan. *Jack-Pine Warbler* 34:127–138.
- NRC (National Research Council). 2000. *Environmental issues in Pacific Northwest: forest management*. National Academy Press, Washington, D.C., USA.
- Odum, E. P. 1941. Annual cycle of the Black-capped Chickadee—1. *Auk* 58:413–333.
- Odum, E. P. 1942. Annual cycle of the Black-capped Chickadee—3. *Auk* 59:499–531.
- Palmer, R. S., editor. 1988. *Handbook of North American birds. Volume 4. Diurnal raptors (part 1)*. Yale University Press, New Haven, Connecticut, USA.
- Peterson, L. 1979. *Ecology of Great Horned Owls and Red-tailed Hawks in southeastern Wisconsin*. Technical Bulletin Number 111. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.
- Possingham, H. P., and I. Davies. 1995. ALEX: a model for the viability of spatially structured populations. *Biological Conservation* 73:143–150.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. *American Naturalist* 132:652–661.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137(Supplement):S50–S66.
- Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165–177.
- Redfield, J. A. 1975. Comparative demography of increasing and stable populations of blue grouse (*Dendragapus obscurus*). *Canadian Journal of Zoology* 53:1–11.
- Reeves, H. M., R. E. Tomlinson, and J. C. Bartonek. 1993. Population characteristics and trends in the western management unit. Pages 341–376 in T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, editors. *Ecology and management of the mourning dove*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Reynolds, R. T. 1989. Status reports: accipiters. Pages 92–101 in *Proceedings of the Western Raptor Management Symposium and Workshop*. National Wildlife Federation, Washington, D.C., USA.
- Reynolds, R. T., S. M. Joy, and D. G. Leslie. 1994. Nest productivity, fidelity, and spacing of northern goshawks in northern Arizona. *Studies in Avian Biology* 16:106–113.

- Reynolds, R. T., and H. M. Wight. 1978. Distribution, density, and productivity of accipiter hawks breeding in Oregon. *Wilson Bulletin* **90**:182–196.
- Robinson, W. B., and E. F. Grand. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. *Journal of Wildlife Management* **22**:117–122.
- Rosenfield, R. N., and J. Bielefeldt. 1993. Cooper's Hawk (*Accipiter cooperii*). In A. Poole and F. Gill, editors. The birds of North America, No. 75. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* **11**:1298–1306.
- Ruckelshaus, M., C. Hartway, and P. Kareiva. 1999. Dispersal and landscape errors in spatially explicit population models: a reply. *Conservation Biology* **13**:1223–1224.
- Sacks, B. N., M. M. Jaeger, J. C. Neale, and D. R. McCullough. 1999. Territoriality and breeding status of coyotes relative to sheep predation. *Journal of Wildlife Management* **63**:593–605.
- Sargent, A. B. 1972. Red fox spatial characteristics in relation to waterfowl predation. *Journal of Wildlife Management* **36**:225–236.
- Sayre, M. W., T. S. Baskett, and R. E. Mirarchi. 1993. Behavior. Pages 161–180 in T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, editors. Ecology and management of the Mourning Dove. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Sayre, M. W., T. S. Baskett, and K. C. Sadler. 1980. Radiotelemetry studies of the Mourning Dove in Missouri. Terrestrial Series 9. Missouri Department of Conservation, Jefferson City, Missouri, USA.
- Sayre, M. W., and N. J. Silvy. 1993. Nesting and production. Pages 81–104 in T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, editors. Ecology and management of the Mourning Dove. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* **77**:1210–1225.
- Schumaker, N. H. 1998. A users guide to the PATCH model. **EPA/600/R-98/135**. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon, USA.
- Scott, J. M., B. Csuti, J. D. Jacobi, and J. E. Estes. 1987. Species richness: a geographic approach to protecting future biological diversity. *BioScience* **37**:782–788.
- Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, S. Caicco, C. Groves, T. C. Edwards, Jr., J. Ulliman, H. Anderson, F. D'Erchia, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs* No. **123**.
- Scott, T. G. 1943. Some food coactions of the northern plains red fox. *Ecological Monographs* **13**:427–479.
- Seidensticker, J. C., and H. V. Reynolds. 1971. The nesting, reproductive performance, and chlorinated hydrocarbon residues in Red-tailed Hawk and Great Horned Owl in south central Montana. *Wilson Bulletin* **83**:408–418.
- Shank, C. C. 1986. Territory size, energetics, and breeding strategy in the corvidae. *American Naturalist* **128**:642–652.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecological Monographs* **38**:31–63.
- Smith, S. M. 1967. Seasonal changes in the survival of the Black-capped Chickadee. *Condor* **69**:344–359.
- Smith, S. M. 1990. Winter replacement rates of high-ranked chickadees vary with floater density. Pages 453–460 in J. Blondel, A. Gosler, J. D. Lebreton, and R. McCleary, editors. Population biology of passerine birds, an integrated approach. NATO ASI Series. Volume G-24. Springer-Verlag, Heidelberg, Germany.
- Smith, S. M. 1993. Black-capped Chickadee. In A. Poole, P. Stettenheim, and F. Gill, editors. The birds of North America, No. 39. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- South, A. 1999. Dispersal in spatially explicit population models. *Conservation Biology* **13**:1039–1046.
- Squires, J. R., and R. T. Reynolds. 1997. Northern Goshawk (*Accipiter gentilis*). In A. Poole and F. Gill, editors. The birds of North America, No. 298. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Steele, M. A. 1999. *Tamiasciurus douglasii*. *Mammalian Species* **630**:1–8.
- Storm, G. L. 1965. Movements and activities of foxes as determined by radio-tracking. *Journal of Wildlife Management* **29**:1–13.
- Storm, G. L., R. D. Andrews, R. L. Phillips, R. A. Bishop, D. B. Siniff, and J. R. Tester. 1976. Morphology, reproduction, dispersal and mortality of midwestern red fox populations. *Wildlife Monographs* **49**:4–82.
- Strickland, D. 1991. Juvenile dispersal in gray jays: dominant member expels siblings from natal territory. *Canadian Journal of Zoology* **69**:2935–2945.
- Strickland, D., and H. Ouellet. 1993. Gray Jay. In A. Poole, P. Stettenheim, and F. Gill, editors. The birds of North America, No. 40. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* **4**(16). [Online: <http://www.consecol.org/vol14/iss1/art16>.]
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl: report to the interagency scientific committee to address the conservation of the Northern Spotted Owl. United States Government Printing Office, Washington, D.C., USA.
- Titus, J. H., J. A. Christy, D. VanderSchaaf, J. S. Kagan, and E. R. Alverson. 1996. Native wetland, riparian, and upland plant communities and their biota in the Willamette Valley, Oregon. Final Project Report to U.S. Environmental Protection Agency. Oregon Natural Heritage Program, The Nature Conservancy, Portland, Oregon, USA.
- Toweil, D. E. 1986. Resource partitioning by bobcats and coyotes in a coniferous forest. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Verner, J. 1965. Breeding biology of the Long-billed Marsh Wren. *Condor* **67**:6–30.
- Verner, J. 1971. Survival and dispersal of male Long-billed Marsh Wrens. *Bird-Banding* **42**:92–98.
- Verner, J. 1975. Interspecific aggression between Yellow-headed Blackbirds and Long-billed Marsh Wrens. *Condor* **77**:328–331.
- Verner, J., M. L. Morrison, and C. J. Ralph, editors. 1986. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Verts, B. J., and L. N. Carraway. 1998. *Land mammals of Oregon*. University of California Press, Berkeley, California, USA.
- Villard, M., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* **13**:774–783.
- Voight, D. R. 1987. Red fox. Pages 379–392 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America*. Ontario Ministries of Natural Resources, Toronto, Ontario, Canada.

- Walley, W. J. 1981. Riding Mountain Whiskey Jacks. *Manitoba Nature Magazine* **22**:14–17, 40.
- Weise, C. M., and J. R. Meyer. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. *Auk* **96**:40–55.
- Wennergren, U., M. Ruckelshaus, and P. Kareiva. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* **74**:349–356.
- White, D., P. Haggerty, J. Baker, and P. Adamus. 2002. Terrestrial wildlife habitat and biodiversity. Pages 124–125 in D. Hulse, S. Gregory, and J. Baker, editors. *Willamette River Basin atlas*. Second edition. Oregon State University Press, Corvallis, Oregon, USA.
- White, D., P. G. Minotti, M. J. Barczak, J. C. Sifneos, K. E. Freemark, M. V. Santelmann, C. F. Steinitz, A. R. Kiester, and E. M. Preston. 1997. Assessing risks to biodiversity from future landscape change. *Conservation Biology* **11**:349–360.
- Wiegand, T., K. A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist* **154**:605–627.
- Wilcomb, M. J. 1948. Fox populations and food habits in relation to game birds in the Willamette Valley, Oregon. Thesis. Oregon State College, Corvallis, Oregon, USA.
- Zwicker, F. C. 1983. Factors affecting the return of young blue grouse to breeding range. *Canadian Journal of Zoology* **61**:1128–1132.
- Zwicker, F. C. 1992. Blue Grouse (*Dendragapus obscurus*). In A. Poole, P. Stettenheim, and F. Gills, editors. *The birds of North America*, No. 15. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Zwicker, F. C., J. F. Bendell, and A. N. Ash. 1983. Population regulation in Blue Grouse. Pages 212–225 in F. L. Bunnell, D. S. Eastman, and J. Peeks, editors. *Symposium on natural regulation of wildlife populations*. Proceedings Number 14. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho, USA.