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A Habitat Network for Terrestrial Wildlife in the Interior Columbia Basin

Abstract

Habitat managers need information about landscape conditions in relation to the composite requirements of species that deserve attention in conservation planning. Consequently, we characterized and mapped a broad-scale network of habitats for five suites of terrestrial vertebrates in the 58 million-ha Interior Columbia Basin (Basin). These five suites, referred to as Families, are composed of 44 species whose habitats have declined strongly from historical (circa 1850-1890) to current periods in the Basin, and thus are of conservation focus. Two of the five Families consist of species that depend on old forests. Species in another Family depend on early-seral forests. Species in the remaining Families depend on sagebrush-steppe or open canopy sagebrush and grasslands. For each Family, we characterized current habitat conditions at the scale of the watershed (mean size of 22,500 ha). Each watershed was classified as one of three conditions. Watersheds in Condition 1 contained habitats whose quality or abundance have changed little since the historical period. By contrast, watersheds in Condition 2 or 3 contained habitats that have changed from historical conditions, but in different ways. Watersheds in Condition 2 had habitats of high abundance but moderate resiliency and quality, whereas watersheds in Condition 3 contained habitats of low abundance or low resiliency and quality. The majority of watersheds (59%-80%) were in Condition 3 for all five Families, whereas the lowest percentage (5%-25%) of watersheds was in Condition 2 for four of five Families. Connectivity among watersheds for all Families appeared low in many parts of the Basin due to spatial gaps associated with areas of habitat extirpation. Our condition maps constitute a broad-scale network of habitats that could be useful for developing multi-species research hypotheses and management strategies for the Basin.

Introduction

Habitats for a myriad of terrestrial vertebrates are declining across the world. Causes for decline are many and varied. Intensive timber harvest, extensive mining, excessive livestock grazing, conversion of habitats to urban and agricultural uses, recreational activities, road access, and widespread invasion of exotic flora and fauna are major causes of decline (Western and Pearl 1989, Noss and Cooperrider 1994). As a result, habitat loss is a major problem for many terrestrial vertebrates. Decline has been especially notable for old-forest, shrub-steppe, grassland, riparian, and wetland habitats (Noss et al. 1995).

In response to these problems, efforts to assess and manage habitats have focused increasingly on large areas, multiple species, and integration of a suite of beneficial management

strategies. For example, The Nature Conservancy has completed over 50 Rapid Ecological Assessments (REAs) since 1991, with each assessment encompassing millions of hectares, hundreds or thousands of plant and animal species, and major biomes containing the world's highest biodiversity (Sayre et al. 2000). Results from REAs now form the basis for broad-scale conservation strategies of The Nature Conservancy across the world.

REAs and similar broad-scale assessments, such as GAP analysis (Scott et al. 1993), are coarse-filter approaches on which habitat management can be based. Coarse-filter approaches assume that conserving representative land areas and habitats over large areas will provide for the needs of all associated species, communities, and ecological processes (Noss 1987, Hunter 1991). By contrast,

fine-filter approaches provide specific habitats for single or few species (Marcot et al. 1994).

Theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969), which led to modern-day principles of conservation biology (Soulé 1986, Noss and Cooperrider 1994) and landscape ecology (Forman and Godron 1987), have direct implications for the design of coarse-filter approaches. That is, coarse-filter approaches must provide habitats of sufficient size, connectivity, quality, and resiliency to withstand the deleterious effects of environmental variation, changing climate, disturbance regime dynamics, demographic stochasticity, inbreeding depression, and Allee effects, all of which contribute to extinction of small or isolated populations (Burgman et al. 1993). If habitats are small, degraded, not connected, or cannot be sustained, the probability of population extinction for species that depend on such habitats increases dramatically (Doak and Mills 1994, Harrison and Fahrig 1995). Moreover, coarse-filter approaches require consideration of habitat needs for a comprehensive set of species associated with environments that have declined or have been degraded (Hunter 1991).

In accordance with these principles, Wisdom et al. (2000) conducted a coarse-filter assessment of 91 species of terrestrial vertebrates in the Interior Columbia Basin (Basin). The 91 species were associated with upland environments and were selected because of empirical evidence of habitat or population decline. Moreover, habitats for these upland species could be mapped accurately with the large pixel size of 1 km² that was available for coarse-filter assessment across the vast area of the 58 million-ha Basin.

As part of their coarse-filter assessment, Wisdom et al. (2000) placed the 91 upland species into 40 groups, and subsequently placed 37 of the groups into 12 Families, using a hierarchical classification system based on similarities in habitat requirements. (Note that the term "Families" has no taxonomic meaning, but instead identifies robust similarities in habitat requirements among large groups of species, regardless of taxonomic relation.) Habitat trends for each of the 91 species, 40 groups, and 12 Families were assessed at multiple spatial scales, using habitat estimates for historical (circa 1850-1890) and current periods. Hann et al. (1997) and Wisdom et al. (2000)

described the innovative methods by which historical and current conditions were estimated in the Basin, and documented the accuracy and sources of uncertainty associated with these methods.

In this paper, we build on the results of Wisdom et al. (2000) to further evaluate habitat conditions for 44 of the 91 upland terrestrial vertebrates in the Basin. We provide rationale for selection of the 44 species, characterize habitat conditions for these species using a coarse-filter approach, and describe the results in relation to relevant theory and implications for management. Within this framework, our goal was to characterize areas for the 44 species where (1) habitats have changed little in quality or abundance from historical conditions; (2) habitats have changed from historical conditions and are of high abundance but of moderate quality and resiliency; and (3) habitats have changed from historical conditions and are of low abundance or low quality and resiliency. These three characterizations constitute a coarse-filter network that could be useful for developing multi-species research hypotheses and management strategies in the Basin. These potential benefits were the primary motivations for our analysis.

Our work was conducted as part of the Interior Columbia Basin Ecosystem Management Project (ICBEMP). The ICBEMP was established in January 1994 through a charter signed by the Chief of the USDA Forest Service (FS) and the Director of the USDI Bureau of Land Management (BLM) (USDA Forest Service 1996). The charter directed that work be undertaken to develop and adopt an ecosystem-based strategy for lands administered by the FS and BLM (FS-BLM) within the Basin. The Science Assessment Area of ICBEMP extends over 58 million ha in Washington, Oregon, Idaho, Montana, and small portions of Wyoming, Nevada, and Utah (Figure 1). Fifty-three percent of the Basin is public land administered by FS-BLM, which was the focus of the ICBEMP.

Study Area

The ICBEMP Science Assessment Area includes all areas drained by the Columbia River within the United States that are east of the crest of the Cascade Range; also included are portions of the Klamath and Great Basins in Oregon (Figure 1).

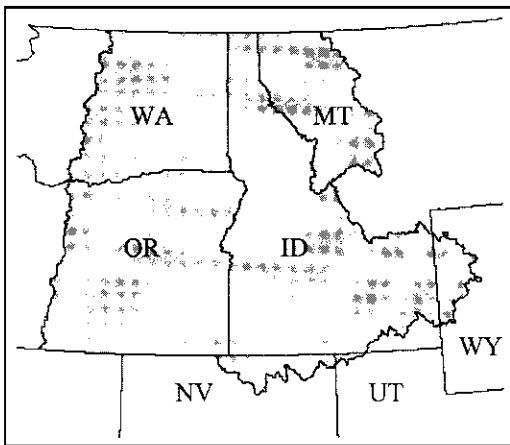


Figure 1. Boundaries of the science assessment area for the Interior Columbia Basin Ecosystem Management Project in the western United States. The science assessment area includes eastern Washington (WA), eastern Oregon (OR), northwest Montana (MT), most of Idaho (ID), and small portions of northwest Wyoming (WY), northwest Utah (UT), and northern Nevada (NV).

The 58 million-ha Basin is subdivided into four spatial scales (Gravenmier et al. 1997): (1) Ecological reporting unit (ERU), (2) subbasin, (3) watershed, and (4) subwatershed. Ecological reporting units, of which there are 13, range in size from about 740,000 to 6,800,000 ha (mean size of approximately 2,375,000 ha). The 164 subbasins average about 345,000 ha, whereas the 2,562 watersheds average about 22,500 ha each. The 7,654 subwatersheds average about 7,700 ha. Quigley et al. (1996) described these spatial scales and the diverse ecological components of the Basin in detail. Marcot et al. (1997), Lee et al. (1997), and Raphael et al. (1998) further described flora and fauna occurring in the Basin.

Methods

Selecting Groups of Species for Analysis

We selected 44 species included in 5 of the 12 Families from Wisdom et al. (2000) for our analysis (Table 1). The five Families included species that depend on low-elevation, old-forest (Family 1), old-forest encompassing a broad range of elevations (Family 2), low-elevation, early-seral forest (Family 4), sagebrush (Family 11), and open-canopy shrubland and grassland (Family 12). We

selected species in these five Families because (1) their habitats have undergone extensive decline or their ranges have contracted substantially since the historical period; (2) their habitats also encompass habitats in decline for species in other Families that were not selected; and (3) their habitat requirements typically are more stringent than species in other Families.

Notably, we did not select species of wide-ranging mammals such as grizzly bear (*Ursus arctos*), gray wolf (*Canis lupus*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). These species are affected strongly by human disturbances, have large home ranges, and require different scales and environmental conditions for conservation planning than do species in the five Families that we analyzed (Raphael et al. 2001). Similarly, we did not select the 82 species associated with riparian, wetland, and other linear or fine-scale features that were identified by Wisdom et al. (2000) as deserving conservation attention in the Basin. Habitats for these species could not be analyzed in a coarse-filter assessment because such fine-scale habitats cannot be mapped accurately with a pixel size of 1 km². Consequently, we assume that different approaches than those used here are needed to characterize environmental conditions for the wide-ranging mammals and the riparian and wetland species identified by Wisdom et al. (2000).

Characterizing Habitat Conditions

Goals and Assumptions

Our goal was to characterize broad-scale conditions that reflected composite differences in the quantity, quality, resiliency, and connectivity of habitats for the 44 vertebrates species of conservation concern that composed Families 1, 2, 4, 11, and 12 (Table 1). A second goal was to focus our characterization in areas containing public lands to facilitate conservation planning on and near such lands. We assumed that our broad-scale conditions could serve as a composite, coarse-filter approximation from which conservation planning could be done over millions of hectares of the Basin in an efficient and effective manner for all 44 species, and for vertebrates in the other Families whose habitats in decline overlap those of the 44. Moreover, we assumed that our

TABLE 1. Common and scientific names of 44 vertebrate species of conservation focus that were selected from Wisdom et al. (2000) for characterization of habitat conditions, and the group and family in which Wisdom et al. placed each species as part of their multi-species assessment.

Family	Group	Common name (<i>scientific name</i>)
1. Old forest, low elevation ¹	1	White-headed woodpecker (<i>Picoides albolarvatus</i>)
	1	White-breasted nuthatch (<i>Sitta carolinensis</i>)
	1	Pygmy nuthatch (<i>Sitta pygmaea</i>)
	2	Lewis' woodpecker (<i>Melanerpes lewis</i>)
	3	Western gray squirrel (<i>Sciurus griseus</i>)
2. Old forest, all elevations ²	4	Blue grouse (<i>Dendrogapus obscurus</i>)
	5	Northern goshawk (<i>Accipiter gentiles</i>)
	5	Flammulated owl (<i>Otus flammeolus</i>)
	5	American marten (<i>Martes americana</i>)
	5	Fisher (<i>Martes pennanti</i>)
	6	Vaux's swift (<i>Chaetura vauxi</i>)
	6	Williamson's sapsucker (<i>Sphyrapicus thyroideus</i>)
	6	Pileated woodpecker (<i>Dryocopus pileatus</i>)
	6	Hammond's flycatcher (<i>Empidonax hammondi</i>)
	6	Chestnut-backed chickadee (<i>Poecile rufescens</i>)
	6	Brown creeper (<i>Certhia americana</i>)
	6	Winter wren (<i>Troglodytes troglodytes</i>)
	6	Golden-crowned kinglet (<i>Regulus satrapa</i>)
	6	Varied thrush (<i>Ixoreus naevius</i>)
	6	Silver-haired bat (<i>Lasionycteris noctivagans</i>)
	6	Hoary bat (<i>Lasiurus cinereus</i>)
	7	Boreal owl (<i>Aegolius funereus</i>)
	8	Great gray owl (<i>Strix nebulosa</i>)
	9	Black-backed woodpecker (<i>Picoides arcticus</i>)
	10	Olive-sided flycatcher (<i>Contopus borealis</i>)
11	Three-toed woodpecker (<i>Picoides tridactylus</i>)	
11	White-winged crossbill (<i>Loxia leucoptera</i>)	
12	Woodland caribou (<i>Rangifer tarandus caribou</i>)	
13	Northern flying squirrel (<i>Glaucomys sabrinus</i>)	
4. Forest stand initiation ³	18	Lazuli bunting (<i>Passerina amoena</i>)
11. Sagebrush ⁴	33	Greater Sage-grouse (<i>Centrocercus urophasianus</i>)
	33	Sage thrasher (<i>Oreoscoptes montanus</i>)
	33	Brewer's sparrow (<i>Spizella breweri</i>)
	33	Sage sparrow (<i>Amphispiza belli</i>)
	33	Lark bunting (<i>Calamospiza melanocorys</i>)
	33	Pygmy rabbit (<i>Brachylagus idahoensis</i>)
	33	Sagebrush vole (<i>Lemmyscus curtatus</i>)
	34	Black-throated sparrow (<i>Amphispiza bilineata</i>)
	34	Kit fox (<i>Vulpes velox</i>)
	35	Loggerhead shrike (<i>Lanius ludovicianus</i>)
12. Grassland, open sagebrush ⁵	36	Col. sharp-tailed grouse (<i>Tympanuchus phasianellus columbianus</i>)
	37	Clay-colored sparrow (<i>Spizella pallida</i>)
	37	Grasshopper sparrow (<i>Ammodramus savannarum</i>)
	37	Idaho ground squirrel (<i>Spermophilus brunneus</i>)

¹ Habitats consist primarily of lower montane forests in late-seral condition.

² Habitats consist primarily of montane to subalpine forests in late-seral condition.

³ Habitats consist primarily of lower montane and montane forests in early-seral condition.

⁴ Habitats consist primarily of sagebrush communities.

⁵ Habitats consist primarily of bunchgrass communities as well as sagebrush and other shrubland communities with open canopies.

characterization of broad-scale conditions could be used for large-scale, long-term conservation planning but would require augmentation at local scales, using fine-scale data on individual species or groups, to ensure appropriate management implementation. Finally, we assumed that our characterization followed principles of conservation biology, in that suitable habitats are identified in terms of composition and structure (as defined by Wisdom et al. 2000), size (as indexed by estimates of habitat abundance), quality and resiliency (as indexed by a disturbance departure variable), and connectivity (as indexed by mapping of spatial gaps), described below.

Habitat Abundance

We used estimates of the number of hectares of habitat from Wisdom et al. (2000) for the 19 groups of the 44 species within Families 1, 2, 4, 11, and 12 (Table 1) to establish three classes of habitat abundance among watersheds for each Family. First, we calculated the mean number of hectares of habitat currently present in each watershed among all groups of species in a Family. Second, for each Family, we ranked the watersheds from highest to lowest, based on the mean number of hectares in each watershed. Finally, we placed the ranked watersheds in three classes: Class A, defined as watersheds with a ranking in the top two quartiles of all watersheds for a Family; Class B, composed of watersheds in the next-lowest quartile for a Family; and Class C, made up of watersheds in the lowest quartile. These three classes represent a ranking of watersheds at three levels of habitat abundance: high (Class A); low-moderate (Class B); and very low (Class C).

Habitat Quality and Resiliency

We combined the three classes of habitat abundance with a variable that reflected habitat quality and resiliency to express the composite quantity, quality, and resiliency of habitat in each watershed for each Family. To estimate quality and resiliency, we used the disturbance departure variable derived by Hann et al. (2002). This variable is a composite estimate of departure from the historical landscape mosaic and succession-disturbance regimes, caused by the cumulative effects of past timber management, excessive livestock grazing, wildfire suppression, road development, agricultural conversions, invasions of

exotic plants, and other human activities that do not mimic historical regimes (Hann et al. 2002). Levels of disturbance departure reflect the degree of coarse-scale change in patch size, composition, and arrangement; frequency and intensity of fire events; timing and severity of tree mortality associated with insect defoliation and pathogen events; successional rates and pathways; timing and intensity of ungulate grazing; composition of native versus non-native vegetation; and human activities and presence. The reader is referred to Hann et al. (2002) for details on the spatial assignment of the disturbance departure variable to watersheds.

Disturbance departure was derived as four classes (low, moderate, high, very high), with very high representing the greatest level of deviation from historical conditions (Hann et al. 2002). A departure class was assigned to each watershed, based on the combination of three broad-scale variables previously developed by Hann et al. (1997): landscape pattern, potential vegetation group, and succession-disturbance regime. Hann et al. (2002) used these three variables to derive the disturbance departure variable, based on their ability to reflect the mid- and fine-scale data concerning change in landscape mosaic and succession-disturbance regimes. Data for these variables are from Hessburg et al. (1999), based on photo-interpreted maps and change in fine-scale features estimated from sample plots.

The disturbance departure variable indexes habitat quality because within-stand composition and structure of vegetation, and among-stand spatial arrangement and pattern of vegetation, are highly correlated with the variables that compose the departure variable. For example, densities of large snags and large logs in forest stands decline with increasing road density, timber harvest, and wildfire suppression (Hann et al. 1997), all of which are correlated with increasing levels of disturbance departure (Hann et al. 2002).

The disturbance departure variable also indexes resiliency because the rate of habitat recovery and the return of desired habitat functions, following disturbance events, are highly correlated with variables that compose the departure variable. For example, resiliency of native vegetation in rangelands is increasingly disrupted by invasion of exotic plants, increasing road density, higher frequency and intensity of wildfire events, and excessive

livestock grazing. All of these factors are correlated with increasing levels of disturbance departure (Hann et al. 2002).

We define resiliency as the capability of system biota and their environments to renew the cycle of functions, processes, and conditions following disturbance, as defined by Hann et al. (1997) from concepts and interpretations of Allen and Hoekstra (1992) and the summary by Noss (2001). Under this definition, habitats of high resiliency have a high probability of maintenance and recovery under disturbance regimes of fire, disease, herbivory, and insect defoliation (Hann et al. 1997, Hann et al. 2002). Use of this definition implies that habitat quality and resiliency are highly correlated. That is, habitats that are not resilient cannot maintain quality over extended time periods.

While our definition of resiliency is compatible with our goal to characterize habitats for broad-scale, long-term conservation planning, habitats that are not resilient also could be important. The long-term contribution of non-resilient habitats, however, would be negligible. Consequently, identification of high-quality but non-resilient habitats requires examination at local scales, using fine-scale data, to ensure appropriate consideration of these habitats over short time periods in relation to our broad-scale characterization of conditions that was designed for long-term planning.

Habitat Conditions

We used the following rules to combine the four classes of disturbance departure with the three classes of habitat abundance to estimate three habitat conditions for each Family during the current period. Condition 1 was defined as any watershed with low disturbance departure, regardless of habitat abundance (class A, B, or C); this condition reflects high resiliency of habitat and a quantity and quality of habitat that is relatively unchanged from historical conditions. Condition 2 was defined as any watershed with moderate disturbance departure and habitat abundance in class A (watersheds within the two highest quartiles of habitat abundance); this condition reflects moderate resiliency, moderate quality, and high quantity of habitat. Condition 3 was defined as any watershed that did not qualify as Condition 1 or 2. Accordingly, Condition 3 occurred in watersheds within the two lowest quartiles of habitat abundance (Class B or C) that had a distur-

bance departure other than low, or in watersheds with habitat abundance of Class A that had a disturbance departure of high or very high; this condition typically reflects habitats of low quantity or low resiliency and quality.

Condition 1 can be thought of as watersheds with habitats similar to historical conditions, while Condition 2 might be considered watersheds with degraded but abundant habitats. By contrast, Condition 3 could be described as watersheds with degraded and uncommon, rare, or extirpated habitats.

We applied our rule set to any watershed, for a given Family, that was within the range of any species in the Family, and that contained habitat for the Family during the historical or current periods. Estimates of species ranges, and of habitat occurrence during historical and current periods, were obtained from Wisdom et al. (2000). Applying our rule set to watersheds that contained habitat for a Family during the historical period was important because many of these watersheds no longer support habitat. This loss of habitat over time would otherwise have been overlooked, thus biasing our evaluation.

While our rule set may appear to combine too many different characteristics in too few categories of habitat condition, we explored a variety of alternative rules for combining the classes of disturbance departure and habitat abundance. We concluded from these explorations that the three habitat conditions were efficient at providing a coarse-filter approximation of the composite differences in habitat quantity, quality, and resiliency for each Family, in accordance with our goals and assumptions. For example, we found that watersheds in Condition 3 typically contained habitats of very low abundance, with a high or very high departure that indicated low or very low quality and resiliency. We also found that habitats had been extirpated in many Condition 3 watersheds, an occurrence unique to this Condition. These characteristics of Condition 3 contrasted strongly with those of Conditions 1 and 2.

Condition Analysis

Use of our rule set resulted in classification of three mutually exclusive habitat conditions among watersheds within the range of species in each Family. Accordingly, we used the rule set to map watersheds in each of the three habitat conditions

for each Family during the current time period. We also calculated the percentage of watersheds in each habitat condition. Finally, we calculated the percent overlap of watersheds in each habitat condition, and all conditions combined, with wilderness areas, roadless areas, and National Parks; this was done to gain insight about the relation between habitat conditions and areas where custodial (non-active) management is a common practice (with the exception of fire suppression, which has occurred in many of these areas [Hann et al. 1997]).

We did not apply the rule set to the small percentage of watersheds (18%) composed entirely of private lands. We excluded such watersheds because (1) our analysis was designed to characterize conditions on public lands, particularly for FS-BLM management; and (2) managers of public lands have no jurisdiction or control over private lands. Private lands, however, are intermixed with public lands in most watersheds that we analyzed, and in these cases, coordination between public and private landowners is more likely to occur. We therefore included all watersheds that contained any amount of public ownership in our analysis. Public lands included all local, state, and federal ownerships; that is, all lands not privately owned.

Identifying Gaps in Connectivity

Although we did not conduct a formal evaluation of habitat connectivity within or across watersheds, we identified the watersheds for each Family that historically contained habitat, but where habitat currently is extirpated or rare, as defined below. Estimates of historical and current occurrence of habitats were obtained from Wisdom et al. (2000).

Watersheds with extirpated habitats were defined as those historically containing habitat but no habitat currently for each Family. Watersheds with rare habitats were defined as those with percent area of habitat $>0\%$ but $<1\%$ for a Family. By mapping and enumerating these watersheds, we could quantify and examine spatial gaps across watersheds where habitats for each Family were absent or nearly absent, but were present historically. We chose to map watersheds with extirpated habitats, and those where habitats were rare, after examining a frequency distribution of habitat area for all watersheds for each Family. This examination revealed a relatively large set of wa-

tersheds with little or no habitat for the current time period that historically contained larger amounts of habitat. Consequently, this mapping exercise was intended to reveal spatial gaps in connectivity that could be addressed through habitat restoration, because such watersheds historically supported a larger amount of habitat for each Family.

Importantly, our estimates of extirpated and rare habitats, as with all our habitat estimates, were based on the large pixel size of 1 km^2 that was used as our mapping unit. With this pixel size, cover types that occur in small patches of $<4 \text{ ha}$ often are not mapped, unless such patches compose $>25\%$ of a given pixel ($>25 \text{ ha}$) (Wisdom et al. 2000). Consequently, relatively small, isolated patches of habitat could still be present in watersheds that we defined as extirpated or rare.

Results

All five Families had the highest percentage of watersheds in Condition 3, which indexed areas of degraded and uncommon, rare, or extirpated habitats (Table 2). Watersheds in Condition 2, which indexed areas of degraded but abundant habitats, composed the lowest percentage of watersheds for four of the five Families (Families 1, 2, 4, and 12, Table 2). Family 11 had the lowest percentage of watersheds in Condition 1, which indexed areas with habitats similar to historical conditions.

Watersheds in Condition 1 had 64%-84% overlap with wilderness areas, roadless areas, or National Parks for all five Families (Table 2). By contrast, watersheds in Conditions 2 and 3 had 7%-23% overlap with these areas. Condition 1 was particularly concentrated in parts of northwest Montana, central Idaho, northeast Oregon, the Cascade Mountains of Washington, southeast Oregon, southwest Idaho, and northwest Wyoming (Figures 2-6). Watersheds in Condition 3 were found across large areas of the Basin, with geographic concentrations varying by Family (Figures 2-6). Watersheds in Condition 2 also varied geographically by Family.

Family 1 (low-elevation, old forest) had a particularly low percentage of watersheds in Condition 1 and high percentage in Condition 3 (Table 2). Watersheds in Condition 3 for this Family were widespread (Figure 2). Notably, watersheds where habitats were extirpated composed 30% of all

TABLE 2. Percentage (number) of watersheds by habitat condition and containing extirpated habitats, rare habitats, and wilderness areas, roadless areas, or National Parks, for five Families of 44 vertebrates species of conservation focus in the Interior Columbia Basin. Habitat conditions and extirpated and rare habitats are defined in the methods.

Family	Habitat Condition	Percentage (Number) of Watersheds			
		By Habitat Condition	With Extirpated Habitats	With Rare Habitats	With Wilderness Roadless Areas or National Parks
1	1	14 (176)	0 (0)	4 (51)	81
	2	6 (73)	0 (0)	0 (0)	7
	3	80 (999)	37 (373)	11 (142)	22
	All	100 (1248)	30 (373)	15 (192)	29
2	1	22 (313)	0 (0)	<1 (4)	84
	2	10 (148)	0 (0)	0 (0)	13
	3	68 (998)	3 (28)	7 (98)	18
	All	100 (1459)	2 (28)	7 (102)	29
4	1	22 (293)	0 (0)	<1 (7)	77
	2	5 (62)	0 (0)	0 (0)	23
	3	73 (955)	35 (333)	6 (75)	17
	All	100 (1310)	25 (333)	6 (82)	30
11	1	15 (189)	0 (0)	<1 (10)	66
	2	25 (310)	0 (0)	0 (0)	20
	3	59 (730)	25 (179)	5 (56)	21
	All	100 (1229)	15 (170)	5 (66)	26
12	1	18 (235)	0 (0)	<1 (6)	64
	2	13 (165)	0 (0)	0 (0)	20
	3	69 (897)	19 (171)	3 (42)	18
	All	100 (1297)	13 (171)	4 (48)	27

watersheds, and all extirpated habitats were associated with Condition 3 (Table 2). Watersheds characterized by rare habitats composed an additional 15% of all watersheds. Watersheds with extirpated and rare habitats for Family 1 occurred mostly in northern parts of the Basin (Figure 2). By contrast, most watersheds in Condition 2 for Family 1 occurred in southwestern areas.

Family 2 (broad elevation, old forest) had a larger percentage of watersheds in Condition 1 than did Family 1, and a smaller percentage in Condition 3 (Table 2). Most watersheds, however, were still characterized as Condition 3, but the percentage of watersheds where habitat was extirpated or rare was lowest of all Families (Table 2). Most watersheds in Condition 2 for this Family occurred in the southwestern parts of the Basin, whereas distribution of watersheds in Condition 3 was widespread (Figure 3).

Family 4 (early-seral forest) had a particularly high percentage of watersheds in Conditions 1 and 3 (Table 2). Extirpated habitats occurred in 25% of all watersheds, and rare habitats occurred in an additional 6% of watersheds (Table 2). Watersheds in Condition 3 were found through-

out the Basin for Family 4, with extirpated and rare habitats concentrated in southwestern and northeastern areas (Figure 4). Watersheds in Condition 2 were largely absent in Oregon and scattered throughout other areas for this Family (Figure 4).

Families 11 (sagebrush) and 12 (open-canopy sagebrush and grassland) had a majority of watersheds in Condition 3 and a low percentage in Condition 1 (Table 2). Extirpated or rare habitats for these Families occurred in 17%-20% of watersheds (Table 2) and were widespread, with the exception of southeast Oregon, where Condition 2 was dominant (Figures 5, 6).

Discussion

Network Characteristics and Patterns

Our results depict broad-scale patterns of habitat conditions for the five Families in the Basin. One important pattern is the high overlap of Condition 1 watersheds with high-elevation wilderness areas, roadless areas, or National Parks for all five Families. Moreover, Condition 1 watersheds compose only 14%-22% of all watersheds among the Families. In combination, these results demonstrate

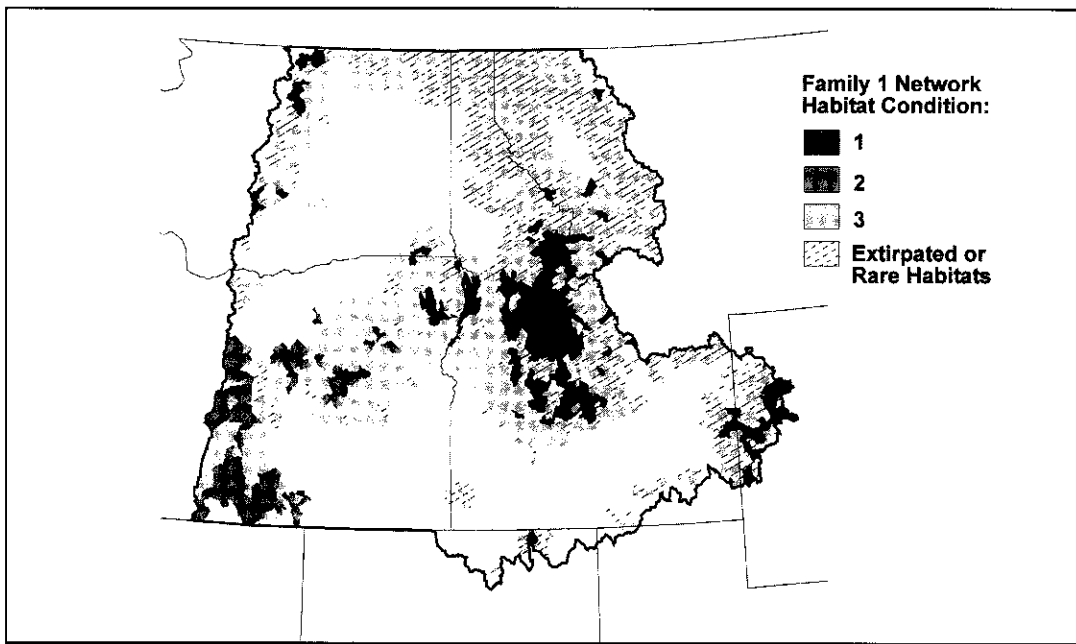


Figure 2. Network for Family 1, composed of low-elevation, old-forest habitats. Watersheds in Condition 1 contain habitats that have undergone little change since the historical period. Watersheds in Condition 2 or 3 have changed since the historical period, but in different ways. Watersheds in Condition 2 are characterized by habitats of high abundance but moderate resiliency and quality. Watersheds in Condition 3 contain habitats of low abundance or low resiliency and quality. Watersheds with extirpated habitats are those containing habitat historically but no habitat currently. Watersheds with rare habitats are those containing $>0\%$ but $<1\%$ of habitat area for the Family. White areas are watersheds that either contain no public lands or are outside the range of species in the Family.

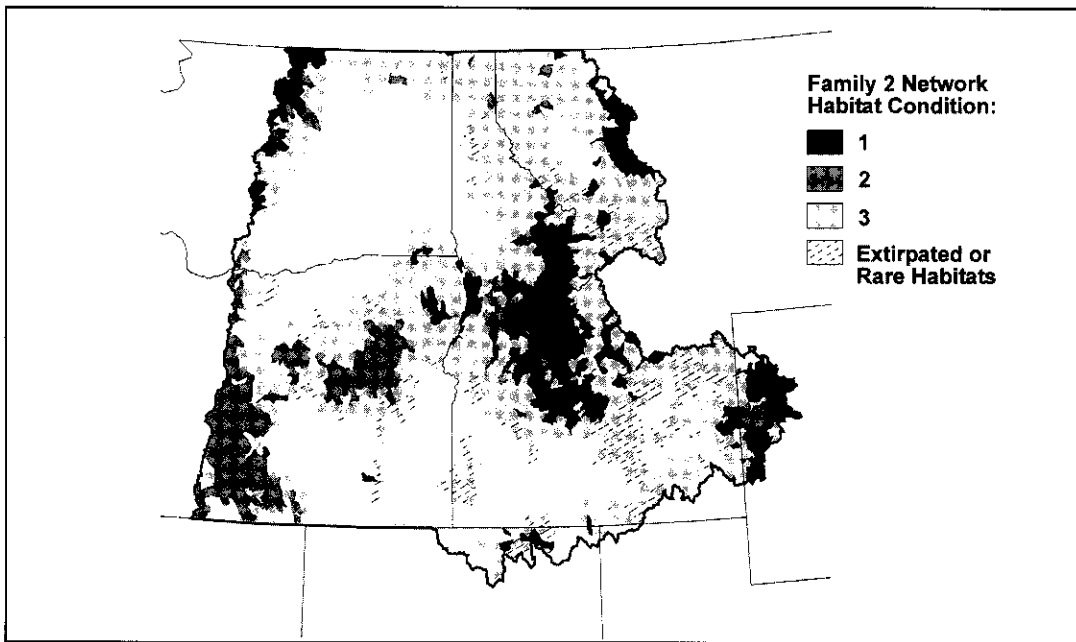


Figure 3. Network for Family 2, composed of broad-elevation, old-forest habitats. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

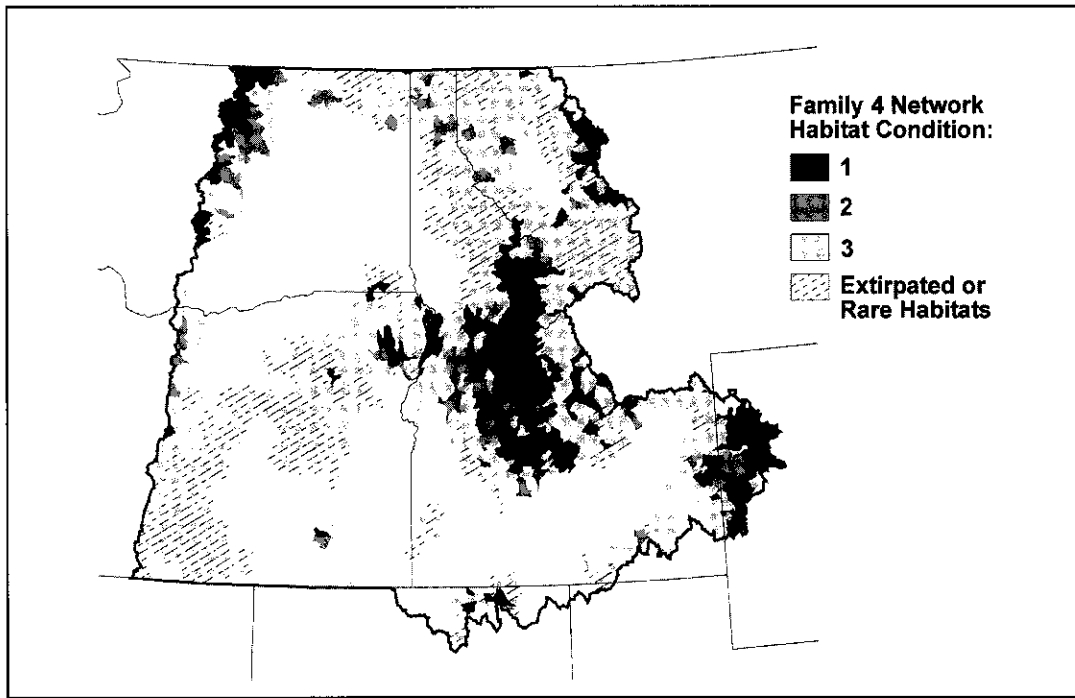


Figure 4. Network for Family 4, composed of habitats of lower montane and montane early-seral forest. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

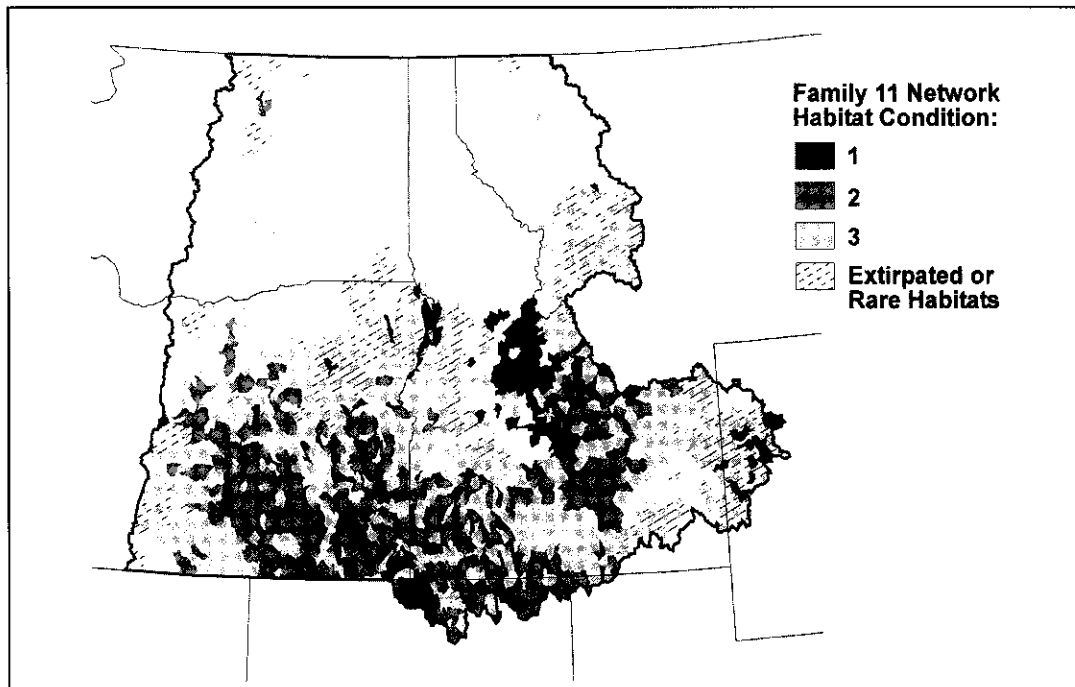


Figure 5. Network for Family 11, composed of sagebrush habitats. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

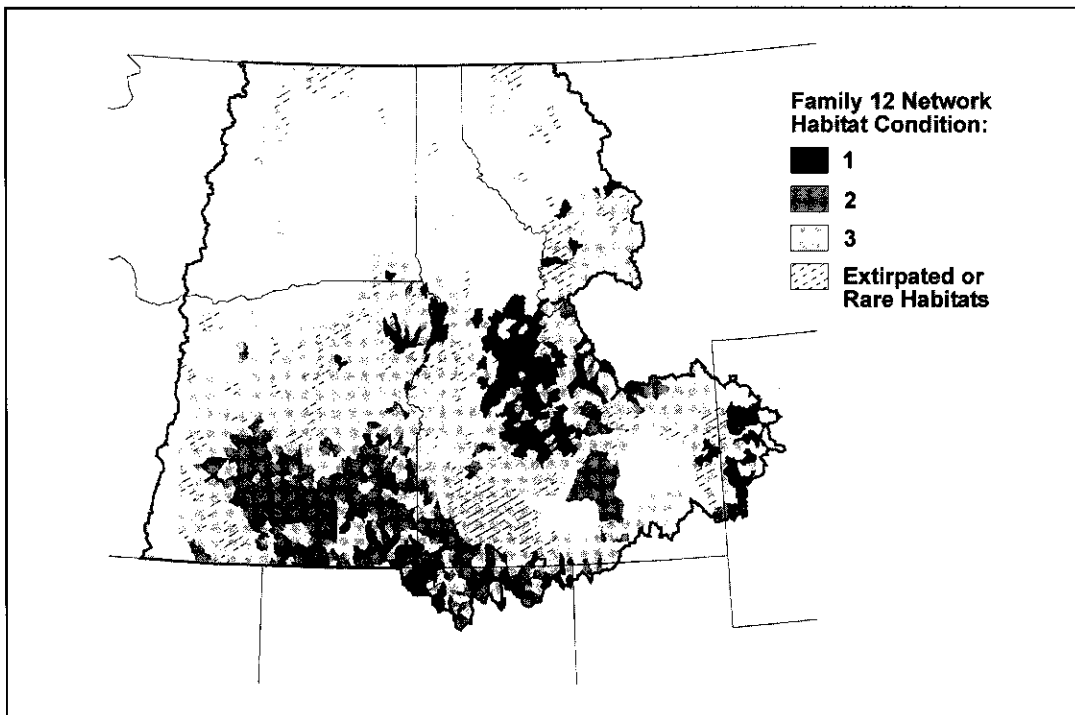


Figure 6. Network for Family 12, composed of open-canopy sagebrush and grassland habitats. Watershed conditions and rare and extirpated habitats for the Family are defined in the caption for Figure 2 and described in the methods.

that wilderness areas, roadless areas, National Parks, and Condition 1 watersheds currently make a small contribution to available habitat for the five Families, and that most of this contribution is in lands that are not actively managed.

A second, complementary pattern is that most habitats for Families 1, 11, and 12 exist at lower elevations in sub-optimal condition (Condition 2 or 3). Moreover, watersheds in Conditions 2 and 3 have small overlap with wilderness areas, roadless areas, or National Parks, and typically have been subjected to intensive timber harvest, intensive grazing by livestock, extensive road development, and widespread fire suppression. This same pattern also exists for Families 2 and 4, but is not as strong as that for Families 1, 11, and 12. In combination, the above results suggest that any conservation approach based solely or mostly on maintenance of Condition 1 watersheds, without explicit consideration for managing watersheds in Condition 2 or 3, would not address the composite needs of species in the five Families.

A third important pattern is the relatively small percentage of watersheds in Condition 2, where

reduced resiliency and quality may limit the long-term presence and suitability of habitat. Although watersheds in Condition 2 make up a relatively small percentage of all watersheds, this condition implies the need to restore disturbance regimes in a manner that can improve resiliency, combined with a need to reduce road density and human disturbance activities in a manner that can improve quality. Consequently, watersheds in Condition 2 may often require active restoration to improve habitat quality and resiliency while maintaining habitat abundance.

Finally, a fourth and perhaps most compelling pattern is the dominance of Condition 3 watersheds for all Families, and the large percentage of these watersheds where habitats have been extirpated. This pattern implies that (1) habitat conservation is critical to protection of small, remnant habitats that dominate many of these watersheds; and (2) habitat restoration is key to increasing the typically low habitat abundance within these watersheds, and to improving the weak habitat connectivity among these and other watersheds. In particular, the restoration of extirpated old-forest,

sagebrush, or grassland habitats will require long time periods, focused planning, sustained implementation, and explicit consideration of the composite needs of species in the five Families within and among the Condition 3 watersheds.

Relation of Theory to Network Characteristics

The connection between principles of conservation biology and their application is not always clear (Doak and Mills 1994). In particular, much debate has focused on landscape issues of patch size, quality, resiliency, connectedness, and human disturbance effects in relation to meeting species needs. For example, whether habitats should be composed of a large number of small reserves (Simberloff and Abele 1976a, 1976b) versus a small number of large reserves (Diamond 1976) is one simplistic illustration of this debate. Such debate continues today, and is magnified by the question of how well theory can be used to meet the composite needs of many species across large landscapes (Shafer 1990, Harrison and Fahrig 1995).

Despite this debate, the combination of theory and empirical data to date provides compelling evidence that a species' persistence depends on suitable habitats of sufficient size and connectedness, sustained indefinitely over large areas that encompass all or most of the species range (Shafer 1990). These conditions buffer the otherwise negative effects of environmental variability, demographic stochasticity, inbreeding depression, and other deleterious processes that cause extinction of small or isolated populations (Burgman et al. 1993).

In that context, our broad-scale network provides both a theoretical and a practical foundation for conservation planning for groups of species that are of conservation focus. Specifically, the network could be used to maintain habitats in a relatively unchanged state from historical conditions (Condition 1), to improve habitats where quality and resiliency have declined (Conditions 2 and 3), to restore habitats in areas of extirpation or low abundance (Condition 3), and to improve connectivity where spatial gaps have developed (Condition 3). Such characterization is a coarse-filter approach, developed for a large set of vertebrates of conservation focus, as summarized over a vast area of the Interior Northwest, for potential use in conservation planning.

For example, a management strategy could be developed from the network information to maintain historical fire regimes in Condition 1 watersheds, helping perpetuate this Condition. Another complementary strategy could emphasize the reduction of road-associated effects in Condition 2 and 3 watersheds, to improve habitat quality and resiliency. A third strategy could focus on conservation of rare habitats in Condition 3 watersheds, with emphasis on protection from imminent management threats, such as those posed by stand-replacing wildfires or by intensive timber harvest. A fourth strategy could outline long-term treatments needed to restore extirpated habitats, thereby improving connectivity over time.

Our network also provides a basis for testing theory as part of adaptive management experiments (Walters 1986). We are unaware of any research hypotheses that have been tested to evaluate the theory, empirical accuracy, and management implications associated with habitat conditions for such a large landscape and large number of vertebrates as that analyzed here. Unfortunately, past research on species of conservation focus, both within the Basin and elsewhere, has largely been fine-scale, single species, observational, not replicated, conducted over short time periods, and not designed to incorporate habitat conditions and associated management actions as treatments.

By contrast, our characterization of a broad-scale network of habitats provides an explicit opportunity for testing multi-species research hypotheses for vertebrates of conservation focus across an extremely large landscape. For example, researchers could hypothesize about multi-species, community-level relations for these terrestrial vertebrates in relation to our habitat conditions, and design and conduct validation research to test these hypotheses. Results of such validation research, if replicated across large areas of the Basin, could provide a rigorous test of the efficacy of our coarse-filter approach for management applications.

Without such multi-species conservation planning and research, the likelihood of extirpation for many vertebrate species in the Basin is high, both for the current time period and under projected management (Raphael et al. 2001). We urge managers and researchers to consider these implications in their future conservation and research designs.

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