

## BIRDS AND CHANGING LANDSCAPE PATTERNS IN CONIFER FORESTS OF THE NORTH-CENTRAL ROCKY MOUNTAINS

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**Abstract.** We describe historical and current landscape patterns for the north-central Rocky Mountains, speculate on the expected consequences of human-induced changes in coniferous forest patterns for birds, and examine the evidence related to the expected consequences. The Rocky Mountain region has one of the most heterogeneous landscapes in North America, combining high complexity in abiotic gradients with fire as a major disturbance factor. In recent decades fire suppression has limited this disturbance, resulting in altered stand structures and relatively homogeneous expanses of mid-successional forest where there were once mosaics of different-aged post-fire stands. Elsewhere, historically homogeneous landscapes that rarely burned have become more heterogeneous due to logging. Many forest types are less common than they were historically due to current management. Land conversion to agriculture and development has primarily occurred in low elevations. We speculate that the consequences of these changes include: (1) bird species adapted to historically homogeneous forest landscapes would be negatively affected by landscape heterogeneity created by timber harvest openings; (2) bird species specialized for forest types that were once prevalent but are now uncommon may be negatively affected by decreasing patch size and increasing isolation; and (3) birds that breed in close proximity to human-added landscape features may be negatively affected by brood parasites or nest predators. Brown Creeper (*Certhia americana*) and Golden-crowned Kinglet (*Regulus satrapa*) had the strongest trends of species sensitive to fragmentation indices. Pine Siskin (*Carduelis pinus*), Chipping Sparrow (*Spizella passerina*) and Dark-eyed Junco (*Junco hyemalis*) were positively associated with fragmentation across most studies. Nesting success varied among landscape configurations, and some trends paralleled abundance patterns. Brown-headed Cowbird (*Molothrus ater*) parasitism rates were extremely low (0–3%) where nest success has been studied in coniferous forests of the north-central Rockies. Across extensive and intensive studies, distance to agricultural lands was the strongest predictor of cowbird presence. Therefore, we found evidence for the ideas that birds adapted to homogeneous forest landscapes have been negatively affected by heterogeneity caused by timber harvesting, that patch size is important for some birds in one vanishing habitat (old-growth ponderosa pine, *Pinus ponderosa*), and that cowbirds are more abundant in conifer forests near human-added landscape features. The effects of changes in landscape patterns on birds in the north-central Rockies seem to be less dramatic than in eastern and midwestern North America, and different landscape measures are more relevant to western conifer forests. We need additional research on most aspects of breeding, nonbreeding, and dispersal ecology in relation to landscape patterns and within-stand changes. We offer our proposed consequences as hypotheses upon which to base future tests.

**Key Words:** birds; fire; fire regimes; fire suppression; forest fragmentation; north-central Rockies; landscape; landscape patterns; wildfire.

Forest fragmentation has clearly affected birds in some landscape configurations in the East and Midwest (Porneluzi et al. 1993, Donovan et al. 1995a, Robinson et al. 1995a). In landscapes where forests are fragmented by agriculture and urbanization, resulting in discrete measurable patches, species richness has been shown to increase with patch area and decrease as patches become more isolated (Whitcomb et al. 1981, Ambuel and Temple 1983, Freemark and Merriam 1986, Blake and Karr 1987). The presence or absence of a species across patches of different sizes suggested minimum area requirements (Temple 1986, Askins et al. 1987, Robbins et al. 1989a). Nesting success declined (Villard et al. 1993, Donovan et al. 1995b), and edge effects (as indicated by nest predation and parasitism) were particularly strong where the landscape matrix had been highly modified (Robinson

1992). These studies identified long-distance migrants as particularly sensitive to area effects.

The effects of landscape changes on bird populations in conifer forests in the West seem to be less dramatic (Rosenberg and Raphael 1986, McGarigal and McComb 1995). Historical and current landscape patterns are quite different in the West than in the East and the Midwest, especially in the mountainous and sparsely populated north-central Rocky Mountains. Conifer forests dominate the mountain slopes of this region, and conversion of lands to agriculture and urban development generally has been restricted to valley bottoms. While the natural heterogeneity of these conifer forests was variable, fire suppression and timber harvest have created landscape patterns with different kinds and levels of heterogeneity. Nonetheless, they remain forested ecosystems that may not present barri-

ers to many native species (McIntyre and Barrett 1992). The response of avian species to this dynamic mosaic may be species-specific and process-specific (Haila 1999). Edge effects may also be substantially different in forest-dominated landscapes than in agricultural ones (Hanski et al. 1996, Bayne and Hobson 1997).

Different measures of landscape patterns are more relevant to landscapes in western conifer forests than those used in the East and Midwest. For example, size and isolation of an individual forest patch is almost impossible to measure in conifer forests of the north-central Rockies because the forest is the matrix rather than the patch, with most stands connected in some way to other conifer forests that may or may not be similar in age, species composition, and structure. The exceptions include rarer forest types, such as old-growth ponderosa pine (*Pinus ponderosa*) or patches of recent fire disturbance. Measures of fragmentation in western conifer forests are thus better achieved by characterizing patterns within a defined landscape, based on relative amounts of forest and amounts and types of edges. More complex variables may be necessary, such as measures of connectivity (Taylor et al. 1993). When patch size is used, patch boundaries often are created somewhat artificially when a user-defined landscape outline is imposed onto the forest matrix for analysis. Because of these constraints, studies in western coniferous forests usually describe the structure of the landscape mosaic in which the forest is embedded (see Wiens 1989) and then relate that structure to avian populations (Rosenberg and Raphael 1986, van Dorp and Opdam 1987, McGarigal and McComb 1995, Schieck et al. 1995).

We investigated whether bird populations are related to landscape changes in north-central Rocky Mountain conifer forests and whether these relationships are similar to what has been reported for other regions. We define the north-central Rockies as that area from eastern Oregon and Washington east through Idaho and western Montana to Wyoming (Fig. 1). We include aspen (*Populus* spp.) in our discussion of conifer forests because it is an integral part of many conifer landscapes. To look at the relationships between birds and landscape patterns, we (1) describe historical landscape patterns and the processes responsible for them; (2) describe current landscape patterns and their causes; (3) discuss implications and potential consequences of human-induced changes between historical and current patterns for coniferous forest birds; (4) examine the current evidence surrounding the expected consequences; and (5) compare our findings for the north-central Rockies to other regions.

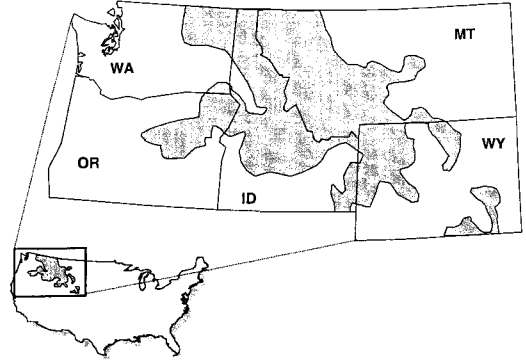


FIGURE 1. The north-central Rocky Mountain geographic area. Rocky Mountain forest type boundaries from Bailey's (1995) ecoregions of the United States, including portions of northern, middle, and southern Rocky Mountain steppe provinces.

### HISTORICAL LANDSCAPE PATTERNS

Natural landscape heterogeneity results from the superposition of a disturbance regime onto vegetation patterns created by abiotic gradients (Turner and Romme 1994). Historically, the north-central Rocky Mountain region had one of the most heterogeneous landscapes of any area in North America due to a dry climate and frequent lightning-caused fires, and this disturbance regime was superimposed on complex vegetation patterns resulting from moisture gradients and finely dissected topography.

Characterizing natural or presettlement landscapes can be a very difficult task (Noss 1985, Sprugel 1991). The evidence is scattered and subject to many potential biases (Noss 1985). In the recent bioregional assessment of the interior Columbia River Basin, Hann et al. (1997) used scattered evidence, expert opinion, and simulation models to estimate broad-scale landscape patterns across the region for the 1850–1900 time period. The mid-scale assessment associated with that project (Hessburg et al. 1999) used historical aerial photographs to characterize landscape conditions in sampled watersheds, but historical photos could be found for only the “recent historical” period of the 1930s to 1960s.

Even if accurate historical data could be recovered for one point in time, the dynamic nature of the disturbance regimes diminishes the usefulness of that information. Fire size and severity depend on previous disturbance history (e.g., fuel buildup) as well as cyclic weather patterns (Bessie and Johnson 1995). There is growing evidence that fire disturbance was extremely variable historically and probably not in equilibrium across the landscape (Sprugel 1991, Turner and Romme 1994, Brown et al. 1999). In addi-

tion, native Americans altered fire regimes for hundreds of years before Euro-American settlement (Barrett and Arno 1982). Therefore, any characterizations of historical landscape patterns must be considered generalizations and take into account the highly variable nature of the landscape.

#### ABIOTIC FACTORS

The north-central Rockies are composed of many mountain ranges of varying ruggedness and orientation. Moisture varies with elevation and topography, and there is also a regional gradient in rainfall due to continental climate patterns (Habeck and Mutch 1973, Peet 1988). Finely dissected topography interweaves land units of very different slopes, soils, moisture retention properties, and exposures, and these patterns occur at several spatial scales. Local landscape vegetation patterns are strongly influenced by these abiotic gradients.

Higher elevations have lower temperatures and receive more precipitation. Annual precipitation in the north-central Rockies ranges from less than 380 mm in intermontane valleys to more than 1500 mm at higher elevations (Habeck and Mutch 1973). These local temperature and moisture patterns create zones of forest habitat types based on the physiological requirements and competitive abilities of the various tree species (Daubenmire 1956). For example, in much of the north-central Rockies, the driest and lowest-elevation forests historically were dominated by ponderosa pine, which remains an important early-seral species up into the mid-elevation zone, where Douglas-fir (*Pseudotsuga menziesii*) was typically the major tree species in climax vegetation. The less drought-resistant Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) compete for climax status only in the more moist, upper-elevation zones. Each of these zones had different fire regimes (Arno 1980). Fire in many of these regimes maintained large areas dominated by shade-intolerant (early-seral) tree species, including ponderosa pine, lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), sometimes grand fir (*Abies grandis*) and Douglas-fir, and, historically, western white pine (*Pinus monticola*).

Local topography and soils can drastically alter available nutrients, solar radiation, temperature, and water retention (Peet 1988, Swanson et al. 1988). South-facing slopes and ridge tops are much warmer and drier and may support vegetation typical of lower elevations, if soils allow. Sheltered valley bottoms have lower solar radiation and may collect water and cold-air pockets that support vegetation more character-

istic of that nearly 500 m higher on open slopes (Peet 1988). Naturally treeless areas occur wherever slopes are too steep or rocky, or where there is prolonged summer soil drought (Daubenmire 1968). Areas on the east side of the Continental Divide especially have widespread occurrence of forest-grassland-sagebrush mosaics, probably regulated by the availability of moisture (Patten 1963) and the frequency of fire (Arno and Gruell 1983).

In contrast, moist Pacific air reaches a limited area in southeastern British Columbia, north-eastern Washington, northern Idaho, and north-western Montana. The resulting luxuriant forests in this region appear similar to forests in the Cascade Mountains (Peet 1988), with tree species including western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and grand fir (Habeck 1987). The combination of greater precipitation and gentler topography results in relatively continuous forests in this region, including the valley bottoms where there is often no well-defined lower timberline.

#### DISTURBANCE

Disturbance imposes further heterogeneity on the landscape, at several spatial scales, by producing a mosaic of age classes and successional communities. Fire was historically the most prevalent natural disturbance in the northern Rocky Mountains (Gruell 1983).

The extent and severity of fires in the north-central Rockies depended on the moisture gradient, which varied temporally as well as spatially (Arno 1980). Forests in more mesic areas burned less often (every 50–300 years; Table 1), so they were more likely to reach later successional stages and to accumulate larger amounts of woody fuels, not burning until sufficient fuels and weather conditions produced a stand-replacing crown fire. Forests in drier areas would burn more often (every 5–50 years; Table 1), before sufficient fuels could accumulate to result in a crown fire. These frequent underburns destroyed seedlings of shade-tolerant tree species while causing minimal harm to fire-resistant early-seral trees, thus maintaining non-climax stands of old-growth ponderosa pine and western larch (Arno et al. 1997).

Historically, old-growth ponderosa pine and western larch dominated millions of acres on drier valley bottoms and south facing slopes throughout much of the north-central Rockies (Arno et al. 1997). Although these “fire-dependent” (Habeck 1988) forests could be extensive, complex topography and moisture gradients usually made these forests less homogeneous than in the Southwest (Arno 2000). Heterogeneity could occur at several scales, with grassland-for-

TABLE 1. REPORTED MEAN AND RANGE OF HISTORICAL FIRE INTERVALS IN GENERAL CONIFEROUS FOREST CLASSES

General habitat class <sup>a</sup>	Description	Mean fire intervals <sup>b</sup> (yrs)	Fire interval range <sup>b</sup> (yrs)	Predominant fire regime <sup>c</sup>
Limber pine	Mostly small stands mixed with grass and shrubs on dry or rocky sites	74	variable	Nonlethal?
Warm, dry ponderosa pine or Douglas-fir	Open stands, with grass understory maintained by frequent fire	5–30	2–55	Nonlethal
Warm, moist ponderosa pine	Typically ponderosa pine dominant with an understory of Douglas-fir in the absence of fire	10–49	3–97	Nonlethal
Cool, dry Douglas-fir	Generally open stands of Douglas-fir with sparse understory	35–40	variable?	Nonlethal
Moist Douglas-fir	Douglas-fir often dominates; closed-canopy ponderosa pine, larch, and lodgepole pine common in seral stages	25–30	8–66	Mixed
Grand fir/mixed conifer	Diverse closed-canopy forest; often develops into mixed species stand	13–120	5–150	Mixed-Lethal
Cool lodgepole pine	Pure stands of lodgepole pine or mixed with grand fir and whitebark pine	24–50	1–88	Lethal-Mixed
Subalpine fir and codominant species	Spruce and other firs common in seral stages; stand-replacement fires common	57–153	50–300	Lethal
Moist redcedar and western hemlock	Closed-canopy stands of redcedar and western hemlock	70–120	25–200	Lethal

<sup>a</sup> General classes of forest habitat types employed by U.S. Forest Service (Steele et al. 1981), arranged approximately on a dry to moist gradient.

<sup>b</sup> Fire-interval estimates from Arno 1980, Arno and Gruell 1983; Arno et al. 1995, 1997; Crane and Fischer 1986, Gruell et al. 1982, Gruell 1983.

<sup>c</sup> Historical fire regime thought to occur over most acreage; all habitat types could have all fire types.

est mosaics at the drier extremes and with denser forests created by stand-replacing fires at the wetter extremes. East of the Continental Divide, where it is too dry for larch and too cold for ponderosa pine, Douglas-fir forests often had similar fire regimes (Arno and Gruell 1983). In very dry years, stand-replacement fires may have occurred in any of these areas (Bessie and Johnson 1995, Brown et al. 1999).

In the more mesic areas of the north-central Rockies (maritime-influenced forests, north-facing slopes, and mid- to high-elevation forest types), the predominant fire regime was one of infrequent, stand-replacement fires (Arno and Davis 1980, Romme 1982, Fischer and Bradley 1987, Barrett et al. 1991). In fact, the origin of most Rocky Mountain forest stands can be traced to stand-replacement fires (Arno 1980).

Historically, most individual fires were small (<1 ha; Strauss et al. 1989), because fuels were too moist or sparse to spread the fire. However, most of the area burned by stand-replacement fires was due to a few large fires in dry years (Strauss et al. 1989, Bessie and Johnson 1995), so it was the large fires that created the vegetation mosaic that dominated the landscape until the next extensive fire (Turner and Romme 1994). Large crown fires rarely consumed an entire forest because of local variations in wind, topography, vegetation type, natural fire breaks, and fuel loads (Turner et al. 1994). These factors produced a heterogeneous pattern of burn sever-

ities, as well as islands of unburned vegetation (Eberhart and Woodard 1987, DeLong and Tanner 1996). The degree of patchiness depended on the dryness of fuels in the year of the fire (Turner et al. 1994, Turner and Romme 1994).

Data on natural fire intervals in different forest cover types suggest that fire severity and frequency were highly variable prior to current fire suppression activities (Table 1). Frequent nonlethal fires and infrequent stand-replacement fires could occur in the same region depending on weather and fuel accumulations, or individual fires may have been of "mixed severity," with many trees dying and many surviving (Brown 1995, Arno 2000). Mixed-severity fire regimes occurred especially in mid-elevation, mixed-conifer forests, where moisture regimes and topography were variable, and fire-resistant tree species (especially larch and ponderosa pine) occurred. Mixed-severity fires produced heterogeneity at several scales, killing variable amounts of trees within a forest stand and affecting variable numbers of stands within a landscape. The moisture regime influenced this variability in size, with drier areas tending to have smaller patches of lethal burns because fires burned often enough to prevent sufficient fuel accumulation for extensive crown fires (Barrett et al. 1991). This typically left a patchy, erratic pattern on the landscape that fostered development of highly diverse communities (Barrett et al. 1991, Arno 2000, Lyon et al. 2000).

## CURRENT TRENDS

In the north-central Rockies, most changes in landscape patterns from historical to current are the result of changes in the disturbance regimes due to fire suppression and timber harvesting. The resulting forests may differ in age, structure, species composition, or landscape pattern, but they remain conifer forests. The little land conversion that has occurred is focused within the lower elevations where forest or grassland has been converted to agricultural land, rural residences, or urban areas.

### FIRE SUPPRESSION

Fire suppression has become increasingly effective since the 1930s (Arno 1980, Barrett *et al.* 1991). Through much of the low and mid-elevation landscapes, fire suppression has altered stand structures and landscape patterns throughout the north-central Rockies (Tande 1979, Arno 1980, Barrett *et al.* 1991). Because dry, lowland areas had fire-return intervals of 5–50 years, the suppression of low-intensity fires for up to 70 yrs has resulted in abnormal fuel accumulations that make the historically resistant old-growth pine and larch more susceptible to stand-replacement fire.

Hann *et al.* (1997) estimated that 19% of the interior Columbia River Basin has changed to a lethal fire regime from mixed or non-lethal over the last century. Complex, uneven-aged stands containing fire-resistant trees are being replaced by even-aged post-fire stands that cover large areas of the landscape (Hann *et al.* 1997). Future fires that burn in this simplified landscape may be larger and more homogeneous, so the homogeneity may be self-perpetuating (Arno 1980, 2000; Barrett *et al.* 1991).

Many areas naturally had heterogeneous landscapes due to a mosaic of successional stages following stand-replacement fires. Here, fire suppression is converting this mosaic of forest stands from a variety of age classes into a more homogeneous expanse of mid-successional mature forest (Hann *et al.* 1997). Because succession changes forest structure most rapidly in the earliest age classes, it has taken only a few decades for fire suppression to allow large expanses of closed-canopy, continuous forest to form on the landscape (Tande 1979). However, in areas with stand-replacement fire regimes, the time period of successful fire suppression may not yet be long enough to greatly affect the historical fire-return intervals of 140 to 400 years (Romme 1982, Barrett *et al.* 1991).

Fire suppression also reduces many unique post-fire habitats on the landscape. Early post-fire patches of standing dead trees are much re-

duced throughout the region. There also has been a loss of shade-intolerant tree species, such as ponderosa pine, larch, and aspen, as succession advances in the absence of fires (Hann *et al.* 1997). Fire-maintained old-growth ponderosa pine stands are an obvious example, but western larch also formed large, open stands of fire-maintained old growth (Arno *et al.* 1997). Larch is restricted to relatively more mesic areas than ponderosa pine, but it is the most shade-intolerant and fire-resistant conifer species in the north-central Rockies (Arno and Fischer 1995), so it is an important early-seral species as well as being an important older-aged component of forests in mixed-severity fire regimes. Aspen is another early-seral tree species that regenerates following fire. In the Centennial Mountains of Idaho, aspen cover has been reduced 80% since 1850, while mature conifer forest increased in area, patch size, and connectivity (Hansen and Rotella 2000). Increasing isolation may be another landscape factor affecting stands of these tree species.

### TIMBER HARVEST

With the suppression of fires, timber harvesting is now the most important disturbance returning conifer forests to early successional stages. It is unclear whether the total area involved is similar, however. Hann *et al.* (1997) estimated that the current areal extent of early-successional stands in moist forests (20%) is at the low end of the historical (pre-1900) range (19–29%), is about the same (18%) as historical in low-elevation dry forests (8–20%), and higher (33%) than historical (23–25%) in upper-elevation cold forests. There are great differences, however, in the landscape patterns and stand structures produced by timber harvest compared with fire (Hann *et al.* 1997). Whether timber harvest increases or decreases landscape heterogeneity depends on the natural heterogeneity of the area (*i.e.*, fire regime and topography), the harvest methods used, and the spatial scale at which analyses are done.

Timber harvest has greatly reduced the accessible, low-elevation dry forests that historically had non-lethal fire regimes and were dominated by old-growth ponderosa pine or western larch. Accessible forests were preferentially logged first, with more distant ones harvested as technology improved and road systems were created (Hejl 1994). Few old-growth stands remain. In the national forests of eastern Oregon and Washington, where the original low- and mid-elevation ponderosa pine forests may have been about 90% old growth, nearly three-quarters of this old growth had been logged by 1970 (Henjum *et al.* 1994). In addition, 82% of the remaining old-

growth patches are smaller than 100 acres, with only 7 patches over 5,000 acres (Henjum et al. 1994). Fire suppression has resulted in further danger to these patches by allowing the buildup of fuels and converting patches to denser forests with more shade-tolerant tree species. Hann et al. (1997) estimated that the ponderosa pine cover type decreased by 26% throughout the interior Columbia River Basin since 1900. Open-canopy old growth has diminished even more (Henjum et al. 1994). Timber harvesting in combination with fire suppression has also reduced old-growth larch on the landscape. Hann et al. (1997) estimated that the western larch cover type (all ages) has decreased by 36% throughout the interior Columbia River Basin since 1900.

Mid-elevation forest with mixed-severity fire regimes historically had a diversity of stand structures and landscape patterns. Timber harvesting returns some patch heterogeneity to these forests, but generally on a coarser-grained scale than produced by natural fires, with a more regular pattern (Reed et al. 1996a). Clearcuts do not retain the remnant trees or snag structure typical of post-fire forests, nor do they create an environment that could maintain the historical complexity of community composition and structure. Consequently, most of the early-seral forest stands within this type are very different in composition and structure relative to the native conditions (Hann et al. 1997). Harvest methods that retain green trees (e.g., Lehmkuhl et al. 1999) may better mimic some mixed-severity fires, but still lack the snag structure or large, downed woody debris. If the same prescription is always used for this type of cutting, it will produce a relatively simplified and homogeneous landscape.

The most productive forests in this region were the "Cascadian" forests around northern Idaho, where fires were rare and, therefore, large blocks of old growth likely developed. Once fairly homogeneous landscapes have been riddled with clearcuts and other logged conditions. In these and other forests with stand-replacement fire regimes, (e.g., high-elevation lodgepole pine), the creation of many small clearcuts is a departure from the pattern of disturbance created by the natural fire regime (Brown 1995). Similarly, in boreal forests in Canada, DeLong and Tanner (1996) found that wildfires created a more complex landscape pattern than clearcut harvesting practices do, with a greater diversity of patch sizes, more irregular shapes and boundaries, and more patches of mature forest intermixed. These patches may be critical for bird species that require heterogeneity in patch structure. They also provide sources of large trees and snags (legacies) within the young post-dis-

turbance forest (DeLong and Tanner 1996). No cutting method can create the dense snag structure that is produced by a stand-replacement fire.

It is unclear if timber harvest has created more fragmentation than natural disturbance regimes. Reed et al. (1996a) found a substantial increase in patchiness created by clearcutting and roads from 1950 to 1993 in high elevation forests in the Medicine Bow Mountains of southern Wyoming. Quantitative landscape indices suggested a level of fragmentation greater than that found in the Oregon Cascades. However, the disturbance patterns in Wyoming were superimposed on a landscape of natural heterogeneity, and it is unknown what the landscape in either 1950 or 1993 would have been like under a natural fire regime. Tinker et al. (1998) found similar results in the Bighorn Mountains of north-central Wyoming. Old-growth forest patches produced by natural disturbances in western coniferous forests were typically much larger and more continuous than are the remnant patches created by timber harvesting and road building (Tinker et al. 1998). However, they found that roads contributed more to this change in landscape indices than did clearcuts. It is not known if roads are wide enough to cause harmful fragmentation effects for most Rocky Mountain bird species, especially in open forests, but roads are certainly a more permanent disturbance than clearcuts (Reed et al. 1996b).

However atypical the landscape pattern produced by timber harvesting may be, it still leads to forest succession and the retention of natural vegetation. A potentially more serious impact on the forested landscape is the permanent conversion of native habitat to agriculture or residential and urban development (including roads). In the north-central Rockies, this conversion has been concentrated in the valley bottoms. While this limits the amount of fragmentation in the overall landscape, these low elevation areas are also the most productive ecosystems for birds (Hansen and Rotella 1999). As rural development accelerates in the inland west (Knight 1997), we may see much more serious fragmentation and edge effects on birds due to added human features on the landscape (e.g., Friesen et al. 1995).

#### PROPOSED CONSEQUENCES OF LANDSCAPE CHANGES ON BIRDS

Based on our knowledge of the historical landscape patterns of the region and the changes that have occurred, we speculate about which birds we would expect to be most affected by landscape changes in the past 100 years in north-central Rockies conifer forests. We offer these speculations as a framework from which to examine the data that exist on bird trends and bird

relationships with landscape patterns. The proposed consequences of landscape changes on birds are: (1) species that are adapted to moist forest types that historically formed the most homogeneous landscapes (e.g., old-growth cedar/hemlock) would be negatively affected by increased landscape heterogeneity created by timber harvest openings; (2) species specialized for forest types that were once prevalent but are now uncommon or rare (i.e., vanishing habitats: aspen, early post-fire forests, old-growth ponderosa pine, and old-growth larch) may be negatively affected by decreasing patch size and increasing isolation over and above the general loss of habitat; and (3) birds that breed in close proximity to human-added landscape features (such as cows, horses, bird feeders, agricultural land, or residential development) may be negatively affected by brood parasites or nest predators that are attracted to these features. More than one of these consequences could be occurring in any one particular landscape.

#### HAS FOREST FRAGMENTATION AFFECTED BIRDS OF THE NORTH-CENTRAL ROCKIES?

To evaluate whether and how coniferous forest birds are affected by changes in landscape patterns, we looked for evidence from each of three sources: (1) regional population trends based on the North American Breeding Bird Survey; (2) studies concerning relationships between bird abundance and specific landscape characteristics, including the effects of logging; and (3) studies concerning relationships between nesting success and human-caused landscape modification.

#### BBS TRENDS

We assumed that if populations of some bird species are declining as the result of changing conditions brought on by fire suppression and intense timber harvesting activities, then the recent 33 years of Breeding Bird Survey (BBS) data (1966–1998) collected from within the region should reflect that fact, although there may be other reasons for any observed declines. Thus, we determined how many conifer forest bird species breed in the north-central Rocky Mountains, which ones are adequately covered by the BBS, and what the BBS data indicated about their recent population trends. We focused our analysis on the Central Rockies region, as defined by Robbins *et al.* (1986), and the conifer forest habitats within that region. By our own estimate, there are 87 bird species that breed in conifer forest habitats within the region (Table 2), and 39 of those (45%) were abundant enough (>1.0 bird per route) and detected frequently

enough (on more than 14 routes within the region) to obtain reasonably reliable models of their population trends (Sauer *et al.* 1999). The bird species for which data are too few, and for which we cannot expect the BBS to provide meaningful results in the future, include those that are rarely detected (e.g., diurnal raptors, grouse), those that occur in habitats that are uncommon and poorly sampled by the BBS (e.g., burned forests), and those that are primarily nocturnal (owls).

Only one of the 39 forest bird species for which the BBS provides adequate coverage appears to be declining significantly in the Central Rockies Region—the Olive-sided Flycatcher (Table 2; see table for scientific names of bird species mentioned throughout text). This species is associated with forest openings (natural and human-created) and edges (Altman and Sallabanks 2000), and was most common in harvested and recently burned conifer forest at sites across northern Idaho and western Montana (Hutto and Young 1999). Of these forest types, burned forests have become rarer within the past century. Because several of the species that were not covered well by the BBS are also relatively common in burned forests (woodpeckers), there is even more reason to focus management attention toward the effects of fire suppression and post-fire salvage logging, both of which have undoubtedly affected the more fire-dependent species negatively (Hutto 1995, Kotliar *et al.* *this volume*).

#### BIRD ABUNDANCE AND LANDSCAPE FEATURES

Very few studies have been conducted that look specifically at the relationships between changing landscape patterns and birds in forests of the north-central Rockies. We identified five data sets that addressed the relationships between the abundances of bird species and some aspect of landscape configuration. These studies were conducted in different forest types, elevation, and climatic regimes as follows: (1) a region-wide correlational analysis based on 312-ha landscapes centered on bird count points across western Montana and northern Idaho, where conifer forest was defined as one category that included all major conifer types and a wide range of canopy closures within those types (i.e., closed canopy, seed tree, shelterwood, and group selection harvested sites; R. Hutto and J. Young, unpubl. report); (2) a correlational analysis of spatial patterns within 300-ha landscapes in mid-elevation closed-canopy mixed-conifer forest, dominated by grand fir/Douglas-fir/ponderosa pine in west-central Idaho (Evans 1995); (3) a comparison of a continuous 240-ha old-growth landscape with two similar-sized old-

TABLE 2. RECENT POPULATION TRENDS OF CONIFER FOREST BIRD SPECIES IN THE CENTRAL ROCKIES REGION AS DETERMINED FROM BREEDING BIRD SURVEY DATA, 1966–1998

Species	No. routes	BBS trend
Turkey Vulture, <i>Cathartes aura</i>		
Sharp-shinned Hawk, <i>Accipiter striatus</i>		
Cooper's Hawk, <i>Accipiter cooperii</i>		
Northern Goshawk, <i>Accipiter gentilis</i>		
Swainson's Hawk, <i>Buteo swainsoni</i>		
Red-tailed Hawk, <i>Buteo jamaicensis</i>	81	3.4*
American Kestrel, <i>Falco sparverius</i>	58	-0.7
Ruffed Grouse, <i>Bonasa umbellus</i>	48	-5.4*
Spruce Grouse, <i>Falcapennis canadensis</i>		
Blue Grouse, <i>Dendragapus obscurus</i>	13	-10.2*
Wild Turkey, <i>Meleagris gallopavo</i>		
Flammulated Owl, <i>Otus flammeolus</i>		
Great Horned Owl, <i>Bubo virginianus</i>		
Northern Pygmy-Owl, <i>Glaucidium gnoma</i>		
Barred Owl, <i>Strix varia</i>		
Great Gray Owl, <i>Strix nebulosa</i>		
Boreal Owl, <i>Aegolius funereus</i>		
Northern Saw-whet Owl, <i>Aegolius acadicus</i>		
Vaux's Swift, <i>Chaetura vauxi</i>		
White-throated Swift, <i>Aeronautes saxatalis</i>		
Black-chinned Hummingbird, <i>Archilochus alexandri</i>		
Calliope Hummingbird, <i>Stellula calliope</i>	39	0.2
Broad-tailed Hummingbird, <i>Selasphorus platycercus</i>		
Rufous Hummingbird, <i>Selasphorus rufus</i>	57	2.0
Lewis' Woodpecker, <i>Melanerpes lewis</i>	11	0.8
Williamson's Sapsucker, <i>Sphyrapicus thyroideus</i>		
Red-naped Sapsucker, <i>Sphyrapicus nuchalis</i>	84	1.0
Hairy Woodpecker, <i>Picoides villosus</i>	74	2.3
White-headed Woodpecker, <i>Picoides albolarvatus</i>		
Three-Toed Woodpecker, <i>Picoides tridactylus</i>		
Black-backed Woodpecker, <i>Picoides arcticus</i>		
Northern (Red-shafted) Flicker, <i>Colaptes auratus</i>	106	0.0
Pileated Woodpecker, <i>Dryocopus pileatus</i>	57	5.4*
Olive-sided Flycatcher, <i>Contopus cooperi</i>	81	-4.0*
Western Wood-Pewee, <i>Contopus sordidulus</i>	90	-0.3
Hammond's Flycatcher, <i>Empidonax hammondii</i>	81	1.7
Dusky Flycatcher, <i>Empidonax oberholseri</i>	91	-2.0
Cordilleran Flycatcher, <i>Empidonax occidentalis</i>	57	2.1
Plumbeous Vireo, <i>Vireo plumbeus</i>	9	-9.9*
Cassin's Vireo, <i>Vireo cassinii</i>	72	1.5*
Warbling Vireo, <i>Vireo gilvus</i>	103	2.2*
Gray Jay, <i>Perisoreus canadensis</i>	67	-0.3
Steller's Jay, <i>Cyanocitta stelleri</i>	59	5.4*
Clark's Nutcracker, <i>Nucifraga columbiana</i>	63	4.6*
Common Raven, <i>Corvus corax</i>	105	2.0
Tree Swallow, <i>Tachycineta bicolor</i>	79	1.7
Violet-green Swallow, <i>Tachycineta thalassina</i>	84	4.0
Northern Rough-winged Swallow, <i>Stelgidopteryx serripennis</i>	64	1.3
Black-capped Chickadee, <i>Poecile atricapillus</i>	94	0.7
Mountain Chickadee, <i>Poecile gambeli</i>	91	0.1
Chestnut-backed Chickadee, <i>Poecile rufescens</i>	25	2.4
Red-breasted Nuthatch, <i>Sitta canadensis</i>	104	3.1*
White-breasted Nuthatch, <i>Sitta carolinensis</i>	32	1.1
Pygmy Nuthatch, <i>Sitta pygmaea</i>	15	1.0
Brown Creeper, <i>Certhia americana</i>		
Rock Wren, <i>Salpinctes obsoletus</i>		
House Wren, <i>Troglodytes aedon</i>	62	3.7
Winter Wren, <i>Troglodytes troglodytes</i>	63	3.0*
Golden-crowned Kinglet, <i>Regulus satrapa</i>	87	0.8
Ruby-crowned Kinglet, <i>Regulus calendula</i>	92	-1.2
Mountain Bluebird, <i>Sialia currucoides</i>	64	1.6



TABLE 2. CONTINUED.

Species	No. routes	BBS trend
Townsend's Solitaire, <i>Myadestes townsendi</i>	<b>80</b>	<b>-0.5</b>
Swainson's Thrush, <i>Catharus ustulatus</i>	<b>103</b>	<b>0.8</b>
Hermit Thrush, <i>Catharus guttatus</i>	72	1.2
American Robin, <i>Turdus migratorius</i>	<b>111</b>	<b>0.5</b>
Varied Thrush, <i>Ixoreus naevius</i>	<b>68</b>	<b>1.4</b>
Orange-crowned Warbler, <i>Vermivora celata</i>	<b>83</b>	<b>1.0</b>
Nashville Warbler, <i>Vermivora ruficapilla</i>		
Yellow-rumped (Audubon's) Warbler, <i>Dendroica coronata</i>	<b>109</b>	<b>-0.5</b>
Townsend's Warbler, <i>Dendroica townsendi</i>	<b>70</b>	<b>1.2</b>
MacGillivray's Warbler, <i>Oporornis tolmiei</i>	<b>96</b>	<b>0.9</b>
Wilson's Warbler, <i>Wilsonia pusilla</i>	<b>77</b>	<b>-1.0</b>
Western Tanager, <i>Piranga ludoviciana</i>	97	-0.8
Green-tailed Towhee, <i>Pipilo chlorurus</i>	13	-2.9
Spotted Towhee, <i>Pipilo maculatus</i>	<b>55</b>	<b>4.5*</b>
Chipping Sparrow, <i>Spizella passerina</i>	<b>111</b>	<b>0.1</b>
Fox Sparrow, <i>Passerella iliaca</i>		
Lincoln's Sparrow, <i>Melospiza lincolni</i>	<b>65</b>	<b>6.8*</b>
Dark-eyed (Oregon) Junco, <i>Junco hyemalis</i>	<b>111</b>	<b>-0.4</b>
Black-headed Grosbeak, <i>Pheucticus melanocephalus</i>	59	8.9*
Lazuli Bunting, <i>Passerina amoena</i>	<b>61</b>	<b>3.4*</b>
Brown-headed Cowbird, <i>Molothrus ater</i>	<b>86</b>	<b>-1.1</b>
Pine Grosbeak, <i>Pinicola enucleator</i>		
Cassin's Finch, <i>Carpodacus cassinii</i>	<b>72</b>	<b>-0.2</b>
Red Crossbill, <i>Loxia curvirostra</i>	<b>79</b>	<b>0.7</b>
Pine Siskin, <i>Carduelis pinus</i>	<b>109</b>	<b>-0.3</b>
Evening Grosbeak, <i>Coccothraustes vespertinus</i>	<b>62</b>	<b>2.2*</b>

Note: Species without trend information were either too rare (<0.1 bird per route) or detected too infrequently (on fewer than 5 routes) to provide estimates; those without bolded data have either deficient regional abundance (<1.0 birds per route) or route sample size (fewer than 14 routes). Species showing significant declines or increases ( $P \leq 0.05$ ) are noted with an asterisk next to the trend value.

growth and selectively-harvested landscapes, each with embedded clearcuts in western redcedar/western hemlock forests in northern Idaho (Hejl and Paige 1994); (4) a comparison of harvested and unharvested 20–100 ha stands of spruce/fir in southeastern Wyoming (Keller and Anderson 1992); and (5) a patch-based study of old-growth ponderosa pine/Douglas-fir/western larch in western Montana (Aney 1984). Not all of the landscape metrics were evaluated in all studies, and two studies (Keller and Anderson 1992, Hejl and Paige 1994) focused more on the overall comparison of landscapes modified by timber harvesting to unmodified areas (see *Effects of logging patterns*). Bird abundances were based on point counts; point locations usually were within conifer forest and encompassed the natural variability in forest cover around points, and analyses generally included only the most common bird species detected. Thus, information is primarily limited to passerines, because other species are not well-sampled by point counts.

#### Amount of forest

The amount of forest covering a landscape is a frequently-reported measure of the degree of fragmentation of that landscape (e.g., Robinson

et al. 1995a). It is one metric that can be measured easily in forested landscapes where the forest remains highly interconnected and occurs as the matrix, not as a patch, although it gives no information on the spatial configuration of the remaining habitat. It also is a measure that can be used over large regions when the resolution of the map used to measure forest cover is too coarse to adequately capture other spatial parameters such as patch shape and edge. In the three landscape studies we considered, forest cover was measured at similar extents (within 200–312 ha areas) and at similar resolutions (at the scale of an aerial photograph or 30 m × 30 m pixel). The forest cover of interest ranged from 3–100% across all sampled landscapes, although these measures are not entirely comparable among studies due to different definitions of “forest.”

A total of 10 species (five residents, three long-distance migrants, and two short-distance migrants) were consistently positively associated with the amount of forest cover in at least one study (Table 3). The probability of occurrence of seven species increased with increasing amounts of conifer forest in the study in which forest was defined most broadly (“all conifer;” R. Hutto and J. Young, unpubl. report). In

TABLE 3. RELATIONSHIPS BETWEEN CONIFEROUS FOREST BIRD SPECIES AND LANDSCAPE METRICS IN THE NORTH-CENTRAL ROCKY MOUNTAINS

	Amount of forest			Patch size			Edge density		Proximity to edge
	All conifer <sup>a</sup>	Mixed conifer <sup>b</sup>	Cedar/hemlock <sup>c</sup>	All conifer	Mixed conifer	Ponderosa pine <sup>d</sup>	All conifer	Spruce fir <sup>e</sup>	Mixed conifer
Positively associated with elements of continuous landscapes									
Vaux's Swift (LDM, CN <sup>f</sup> )					+				
Gray Jay (R, OCN)				(+)					
Chestnut-backed Chickadee (R, CN)	+						-		
Red-breasted Nuthatch (R, CN)	+			+	+		-		-
Brown Creeper (SDM, EN)		+	+		+	+		-	
Winter Wren (R, EN)	+		+	+			-		
Golden-crowned Kinglet (R, OCN)	+	+	+	+	+		-		-
Swainson's Thrush (LDM, OCN)	+			(+)			-		
Hermit Thrush (SDM, OCN)				(+)				-	
Varied Thrush (R, OCN)	+			+			-		
Yellow-rumped Warbler (SDM, OCN)		+			+				
Townsend's Warbler (LDM, OCN)	+			+	+		-		-
Black-headed Grosbeak (LDM, OCN) <sup>g</sup>		+							
Pine Grosbeak (R, OCN)				+					
Mixed associations with fragmentation									
Cassin's Vireo (LDM, OCN)		-				+			
Clark's Nutcracker (R, OCN)	-						+		
Western Tanager (LDM, OCN)	-	+		-					
Negatively associated with elements of continuous landscapes									
Hammond's Flycatcher (LDM, OCN)				-					
Dusky Flycatcher (LDM, OCN) <sup>g</sup>					-				
Common Raven (R, OCN)	-			(-)			(+)		
Mountain Chickadee (R, CN)	-			-			+		
Ruby-crowned Kinglet (SDM, OCN)	-			-			+		
Townsend's Solitaire (SDM, OCN)							(+)		
MacGillivray's Warbler (LDM, OCN) <sup>g</sup>					-				
Chipping Sparrow (LDM, OCN)	-			-			+		+
Dark-eyed Junco (SDM, OCN)	-	-		-					+
Cassin's Finch (R, OCN)	-			-			+		
Red Crossbill (R, OCN)				-			+		
Pine Siskin (R, OCN)	-			-			+	+	+

Notes: Forest types described in text. Not all landscape metrics evaluated in all five forest types. Positive association (increased abundance) denoted by +; negative association by -. Responses in parentheses significant at  $0.05 < P < 0.10$ . All others significant at  $P < 0.05$ .

<sup>a</sup> R. Hutto and J. Young, unpubl. report. "All Conifer" forest includes seedtree, shelterwood, and group selection harvested sites.

<sup>b</sup> Evans 1995. Mixed conifer is closed canopy mature mixed conifer.

<sup>c</sup> Hejl and Paige 1994.

<sup>d</sup> Aney 1984.

<sup>e</sup> Keller and Anderson 1992.

<sup>f</sup> LDM = long distance migrant, SDM = short distance migrant, R = resident (as defined by Partners in Flight); EN = enclosed nest, OCN = open cup nest, CN = cavity nest.

<sup>g</sup> Black-headed Grosbeak and Dusky Flycatcher classified as riparian by Hutto and Young 1999; MacGillivray's Warbler excluded from "All Conifer" analyses—not restricted to conifer.

closed-canopy mixed conifer forest, five species increased in relative abundance as amount of forest increased (Evans 1995). Three species were more abundant in unharvested cedar/hemlock landscapes than in harvested landscapes, and were less abundant than expected in harvested areas based on the amount of forest remaining (Hejl and Paige 1994). Across these studies, Golden-crowned Kinglet was most frequently associated with forest cover; Brown Creeper and Winter Wren associations appeared in two studies. The relationship between abun-

dance and amount of forest was not tested directly in spruce/fir (Keller and Anderson 1992), but five species were more abundant in continuous forest than in areas interspersed with clearcuts (see *Effects of logging patterns*).

A similar number (9) of species had the opposite association, decreasing in abundance with increasing amounts of forest, suggesting that they would have a positive response to fragmentation. However, this negative association with forest area was examined directly in only two studies, and there was less correspondence be-

tween these studies. Dark-eyed Junco was the only species that was negatively associated with forest cover in both studies; Western Tanager had opposing associations. More resident species (five) were negatively associated with increased amount of forest than long- (two) or short-distance (two) migrants.

#### *Patch size*

Relationships of abundance with patch size (the area of a continuous block of similar habitat) were tested directly in three studies (Table 3). Most of the species positively associated with larger patch size in the two landscape studies (Evans 1995; R. Hutto and J. Young, unpubl. report) also were associated with amount of forest. The two variables were strongly correlated ( $r = 0.69$ ) in Hutto and Young's study, as they probably are in many western studies. However, Vaux's Swift, Gray Jay, Hermit Thrush, and Pine Grosbeak were associated with patch size but not to amount of forest in these studies (Evans 1995; R. Hutto and J. Young, unpubl. report). Red-breasted Nuthatch, Golden-crowned Kinglet, and Townsend's Warbler had the most consistent positive associations with patch size between the two studies.

Interpreting Aney's (1984) study in old growth ponderosa pine, we identified two species (Solitary Vireo [now Cassin's Vireo] and Brown Creeper) with possible minimum patch size requirements. These species were absent from stands below a certain size, even though those stands might have been large enough to accommodate at least one territory. Cassin's Vireo (reported territory size of 0.5 ha/pair; Aney 1984) was not detected in stands less than 5 ha (9 of 19 stands examined), but was consistently detected in larger stands. Brown Creeper (territory size ranges from <1 to 6.4 ha/pair; Hejl *et al.* 2002) was absent from stands less than 4.5 ha (8 of 19 stands). Many species in this study were not detected frequently enough for a pattern of area sensitivity to emerge. In addition, Aney (1984) did not consider annual turnover in assessing presence or absence within patches (Freemark *et al.* 1995).

Most species (7 of 9) negatively associated with amount of "all conifer" forest across western Montana and northern Idaho (R. Hutto and J. Young, unpubl. report) also were negatively associated with increasing patch size, with the exception of Clark's Nutcracker and Dark-eyed Junco (Table 3). Hammond's Flycatcher and Red Crossbill also were negatively associated with patch size in this study. Only three species decreased in abundance as patch size increased in west-central Idaho (Evans 1995).

#### *Edge*

Relationships between birds and edge density or distance from edge were evaluated in three studies. In "all conifer" forests (R. Hutto and J. Young, unpubl. report), all seven of the species that were positively associated with the amount of forest were also negatively associated with edge density (see Table 3;  $r = -0.048$  between these two predictor variables, demonstrating low correlation, and thus reasonable independence, between them). In this instance, edge was defined as the boundary between patches of dissimilar cover, with 15 possible cover classifications (5 forest types, 4 open land types, 3 riparian types, and 3 other classes) within 312-ha landscapes. Two species (Brown Creeper and Hermit Thrush) had a negative association with edge density in spruce/fir (Keller and Anderson 1992). Evans (1995) measured sensitivity to edge directly by comparing abundance across three distances to edge (<50 m, 50–100 m, >100 m). Edges were defined by openings in closed-canopy forest and the juxtaposition of forests of different ages and canopy closure. Red-breasted Nuthatch, Golden-crowned Kinglet, and Townsend's Warbler were significantly more abundant as distance from edge increased (Table 3).

Across studies, 10 species increased in abundance as edge density increased or distance from edge decreased (Table 3). Chipping Sparrow and Pine Siskin were most frequently positively associated with edge across studies.

#### *Effects of logging patterns*

Two studies in the north-central Rockies (Keller and Anderson 1992, Hejl and Paige 1994) compared the numbers of birds in landscapes modified by timber harvesting to unmodified areas. In both studies, the modified areas were created by logging (stripcuts, spot cuts, and clearcuts) interspersed within previously unlogged or partially-logged forest. (Partially-logged forest remained as continuous forest, but some trees had been selectively removed previously.) The two studies differed in habitat and methodology. In the high elevation Engelmann spruce/subalpine fir study, Keller and Anderson did not sample clearcut areas because they did not want stand comparisons to reflect avian use of unforested areas compared to forested areas. In the low elevation western redcedar/western hemlock study, Hejl and Paige sampled the complete landscapes, allowing points to fall in clearcuts, on edges, or in forest interior, to see how birds responded to clearcut/forest landscapes as a whole.

Of 16 species detected in spruce/fir and 38 species in cedar/hemlock, 9 species were com-

mon to both studies. Of these nine species, three had the same results: Brown Creepers were more abundant in unlogged landscapes, Red-breasted Nuthatches were similarly abundant in logged and unlogged landscapes, and Pine Siskins were more abundant in logged landscapes. Hermit Thrush, American Robin, and Yellow-rumped Warbler had opposite trends in the two studies. Of those species found only in one study but with significant associations, three species were more abundant in unlogged landscapes (Mountain Chickadee, Winter Wren, Swainson's Thrush) and nine in logged landscapes (Northern Flicker, Olive-sided Flycatcher, Townsend's Solitaire, Cassin's Vireo, Warbling Vireo, Orange-crowned Warbler, MacGillivray's Warbler, Western Tanager, and Chipping Sparrow).

In both of these studies, it was difficult to ascertain whether the associations with logged or unlogged landscapes were caused by a simple decrease or increase in suitable habitat caused by logging or by the changes in landscape conditions (i.e., decreased patch size, increased edge). The fact that three species (Brown Creeper, Winter Wren, and Golden-crowned Kinglet) were less abundant in harvested cedar/hemlock landscapes than would be expected based on the amount of forest remaining (see above under *Amount of forest*) suggested that landscape changes could at least be a partial cause of lower numbers in those landscapes. In addition, while most of the species identified in the two studies have similar trends to those resulting from logging in stand-level studies throughout the West (as summarized by Hejl et al. 1995), Gray Jay, Red-breasted Nuthatch, and Pine Siskin do not, indicating potential landscape effects.

### *Synopsis*

Given that there was virtually no replication of any of the conditions among the studies that we summarized, we suggest that the species most or least sensitive to fragmentation, based on their patterns of abundance, are those that show a consistent response in several forest types and geographic regions. Based on this assumption, Brown Creeper clearly had the strongest trend of species sensitive to changes in landscape patterns, as it was associated with at least one variable indicating landscape change (and usually more than one) in four of the five studies examined (Table 3). Golden-crowned Kinglet, Red-breasted Nuthatch, Winter Wren, Hermit Thrush, and Townsend's Warbler also showed consistent results across studies. These species appear as sensitive to disruptions in the pattern of forest cover on the landscape elsewhere in the West. Brown Creeper, Winter Wren, and Red-breasted Nuthatch were correlated with

the amount of forest and/or patch size in coastal Douglas-fir or cedar/hemlock forests (Rosenberg and Raphael 1986, McGarigal and McComb 1995, Schieck et al. 1995), and Red-breasted Nuthatches and Townsend's Warblers avoided edges (Rosenberg and Raphael 1986).

Fewer species had consistent positive associations with elements of more fragmented landscapes in the north-central Rockies. Several species had consistent associations with more than one landscape element within a study, but only three species (Pine Siskin, Chipping Sparrow and Dark-eyed Junco) were consistent across studies. These three species were also more abundant in logged landscapes (Keller and Anderson 1992, Hejl and Paige 1994). Our results were somewhat inconsistent with other western studies. Chipping Sparrow was associated with edges in Douglas-fir forests in California (Rosenberg and Raphael 1986), but Pine Siskin and Dark-eyed Junco were positively associated with larger patches of old-growth Douglas-fir and hemlock forests on Vancouver Island (Schieck et al. 1995).

While the five studies we reviewed differed in methods, particularly in how forest cover was defined, none attempted to define "fragmented" based on a minimum patch size. Thus, inconsistent results among these studies are not attributed to one study considering a 200-ha patch to be a fragment and another considering it continuous forest. Two studies (Evans 1995; R. Hutto and J. Young, unpubl. report) measured fragmentation indices as continuous variables across 300-ha landscapes and related bird abundances in correlation or regression tests. One logging study also based landscape descriptions on 240-ha landscapes (Hejl and Paige 1994). The other logging study used some small (20–40 ha) patches as unmanaged controls (Keller and Anderson 1992), but we used only an edge measure from this study. The old-growth ponderosa pine patch-based study included very small patches (<4 ha) but the only variable discussed from that study was patch size; we used a species' presence or absence across the range of patches as an indication of sensitivity to patch size.

### DEMOGRAPHIC RELATIONSHIPS WITH LANDSCAPE FEATURES

Several studies have suggested that the number of individual birds can temporarily increase in areas adjacent to recent cuts due to displacement of birds into the nearest suitable habitat (Schmeigelow et al. 1997, Walters 1998). Over the long term, high abundances can be maintained from source habitats and a population trend would not be apparent (Van Horne 1983, Vickery et al. 1992). Increased densities could

have a negative impact on reproductive rates through reduced pairing success, competition for resources, and reproductive failure (Hagen et al. 1996), issues for which demographic studies are needed. Data on the effects of landscape patterns on bird demography are seriously lacking from conifer forest habitats in the north-central Rockies. Several recent studies are beginning to provide information to address this gap.

S. Hejl (unpubl. data) studied nesting success of cavity-nesting and enclosed-nesting species in a continuous old-growth (>170 yr) cedar/hemlock forest landscape (240 ha) and compared results to nesting success from a landscape composed of recent clearcuts in a matrix of old-growth cedar/hemlock in northern Idaho. Nesting success did not differ between landscapes for any of the five focal species (Red-naped Sapsucker, Chestnut-backed Chickadee, Red-breasted Nuthatch, Brown Creeper, and Winter Wren) in 1992–1994, but four species (all but Winter Wren) had trends of lower nesting success in the logged landscape. The sample of nests was limited, and the numbers for some species-landscape combinations may be too low to compute reliable Mayfield estimates (Hensler and Nichols 1981).

D. Evans and colleagues (unpubl. report) studied nesting success of Swainson's Thrushes and Western Tanagers in mixed-conifer forests in west-central Idaho. Data were obtained from 10 separate study plots, four of which were classified as located within relatively continuous forest areas and six of which were classified as relatively fragmented. Stands were classified based on a multivariate analysis of landscape cover within 1 km of the avian demography study plots. Nesting success of neither Swainson's Thrush nor Western Tanager differed between landscape classes, although there was a trend for lower success of Swainson's Thrushes, and higher success of Western Tanagers, in fragmented landscapes. However, overall nest success estimates for both species in either landscape class were substantially below the minimum nest success thresholds suggested as needed to support self-sustaining populations (Martin et al. 1996). Evans et al. (unpubl. report) also found no relationship between nest success and distance to edge for either species. Using survival (recapture and resighting of color-marked individuals) and productivity data collected from mixed-conifer habitats in Idaho, they modeled continuous-landscape and fragmented-landscape populations of Swainson's Thrushes and Western Tanagers. Population trajectories did not differ between continuous and fragmented landscapes for either species, and all populations declined rapidly. Because overall estimates of annual sur-

ivorship were relatively high (0.67–0.68 annual survivorship), the authors concluded that the declines in simulated populations were mostly tied to relatively low nesting success.

Sallabanks et al. (1999) initiated a regional study examining the effects of landscape composition on avian nesting success. They monitored replicate plots in managed forest landscapes with both silviculture and agriculture, managed forest landscapes with active silviculture only, and unmanaged forest landscapes with neither agriculture nor silviculture. Although statistical analyses have yet to be conducted, a preliminary examination of the data (2,847 nests of 66 bird species) suggests a mix of results: several species tend to have increasing rates of nest success along a spectrum from managed landscapes with both silviculture and agriculture to unmanaged landscapes (e.g., Warbling Vireo), others appear to be unaffected by landscape composition (e.g., Dusky Flycatcher), and still others have their highest success in the most heavily managed landscapes (e.g., MacGillivray's Warbler; R. Sallabanks, pers. comm.).

The primary cause of landbird nest failures within the north-central Rockies region is predation, as reported elsewhere (Martin 1993). In Idaho, predators destroyed 31–35% of all nests monitored, depending on species and landscape classification (D. Evans et al., unpubl. report). Based on opportunistic observations, these authors recorded evidence of red squirrel (*Tamiasciurus hudsonicus*) predation and speculated that avian predators, such as jays, accounted for some losses. In addition, only one of 202 nests had evidence of cowbird parasitism. Based on one year of data, R. Sallabanks et al. (unpubl. report) reported that 43% of total nests (76% of failures) were destroyed by predators in three regions in Idaho and Montana. In a companion study in west-central Idaho using artificial nests baited with clay eggs, Warner (2000) identified deer mouse (*Peromyscus maniculatus*), yellow-pine chipmunk (*Tamias amoenus*), red squirrel, and northern flying squirrel (*Glaucomys sabrinus*) as the primary predators of nests placed on the ground and in shrubs. Predator assemblages were similar between managed (i.e., with agriculture and/or silviculture) and unmanaged (i.e., without agriculture or silviculture) forest landscapes. Warner (2000) also documented attempted predation on clay eggs by deer, sheep, domestic cattle, coyotes, ground squirrels, beaver, and other songbirds.

Demography data show some consistency with results based on abundance. Abundance data indicated that 14 species are potentially negatively affected by landscape changes caused

by timber harvesting (i.e., numbers for these 14 species are either positively correlated with more or larger forests or negatively correlated with edge density or distance to edge; Table 3). For the four of these 14 species for which we have preliminary nesting success data, three (Brown Creeper, Red-breasted Nuthatch, Swainson's Thrush) had lower nesting success trends in logged landscapes. The other species (Winter Wren) had inconsistent nesting success trends. One of the species with a mixed association with landscape changes according to abundance data (Western Tanager) had a trend of greater nesting success in fragmented landscapes. This latter result was consistent with findings by Davis (1999) that Western Tanagers in Idaho were most closely affiliated with relatively open stands of primarily Douglas-fir trees.

#### *Brown-headed Cowbird occurrence*

Given that nest parasitism has been shown to be a problem in some fragmented landscapes, we summarized the response of Brown-headed Cowbirds to landscape changes. Studies in the north-central Rockies that have examined cowbird abundance within a landscape context consistently show that proximity to agricultural areas is a strong, if not the strongest, predictor of cowbird occurrence (Hejl and Young 1999, Young and Hutto 1999, Tewksbury et al. 1999). Within conifer forest sites across western Montana and northern Idaho, cowbirds were more likely to be found in xeric forests (especially ponderosa pine), in areas with an abundance of cowbird hosts, close to developed, agricultural, and riparian areas, and less likely to be found in subalpine forests (Young and Hutto 1999). In the Bitterroot Valley, Montana, Brown-headed Cowbird abundances were greatest in riparian areas, less in xeric conifer forest, and least in riparian conifer forests (Tewksbury et al. 1999). Within 518-ha landscapes in xeric ponderosa pine/Douglas-fir forests, landscape context was more important than stand attributes in determining cowbird numbers (Hejl and Young 1999). Cowbirds were more abundant in landscapes with more open land (agricultural land and grassland), deciduous riparian habitat, mature forest (70–120 yr), and less old growth. Forest cover, logged openings, human residences, and elevation were not important predictors of cowbird numbers in these xeric forests. All of these studies suggest that cowbird distribution is limited by the presence and distribution of largely supplemental food supplied by human activities. In addition, cowbirds may be more abundant in conifer stands near riparian areas (but not in canyons or riparian conifer forests) because they are attracted to riparian habitats that are dense with

potential hosts, and venture into adjacent conifer forests secondarily.

Fewer data are available to assess the impact of cowbirds on nest success. From BBIRD sites across the West, forest coverage correlated inversely with nest parasitism within 10-km radius areas, with lower parasitization rates where forest coverage was greater (Hochachka et al. 1999). However, the opposite trend was seen at the 50-km scale. Hochachka et al. (1999) hypothesized that this contrary result suggests that traits other than forest cover, such as human-induced land-use practices that are related to forest cover (see Tewksbury et al. 1998), may be responsible for these results.

Where reproductive success has been studied in coniferous forests of the north-central Rockies, cowbird parasitism rates were extremely low (e.g., 0–3% in varied locations in west-central Idaho, northern Idaho, and western Montana; D. Evans et al., unpubl. data; S. Hejl, unpubl. data; R. Sallabanks, unpubl. data). Parasitism rates are likely to be much higher where cowbirds are more abundant, such as in ponderosa pine forests near residential development and agricultural areas. Overall, however, locations supporting higher parasitism rates currently are relatively rare in the coniferous forest landscape of the north-central Rockies.

#### DISCUSSION

We found scattered evidence in the few landscape studies from the north-central Rockies supporting our expectations of the birds most affected by landscape changes. We believe that the "Cascadian" forests of northern Idaho historically were continuous, and extensive logging and consequent fragmentation would result in landscape conditions for which species found there are not well adapted. In fact, the two species (Brown Creeper, Golden-crowned Kinglet) that were negatively associated with fragmentation indices in at least three studies in the north-central Rockies were most commonly affiliated with moist, continuous habitats. Additionally, the trend for nesting success of Brown Creepers in a fragmented landscape was half that of continuous forest (although based on a small sample size; S. Hejl, unpubl. data). Other species associated with moist, once-continuous forests (and therefore ones that we would expect to be affected similarly by landscape changes) are: Chestnut-backed Chickadee, Winter Wren, Varied Thrush, and Townsend's Warbler in cedar-hemlock forests. Much of the high-elevation spruce-fir zone also produced large expanses of continuous forest, where the topography permitted, because of the long period between fires (often 300 yr; Romme 1982). For this reason, bird

species associated with spruce-fir forests, such as Boreal Owl, Hermit Thrush, and Pine Grosbeak, might be sensitive to fragmentation. Several of the above species had our expected associations with fragmentation indices, but in other forest types. Boreal Owl was not reported in the studies summarized.

Whereas the “Cascadian” forests described here are similar to Pacific Northwest forests in structure, landscape, tree species, and bird communities, these moist forests make up a relatively small proportion of the north-central Rockies as a region. Given the greater natural heterogeneity in the north-central Rockies, it follows that overall, fewer species may exhibit a negative association with fragmentation here than in the Pacific Northwest.

Mid-elevation forests, primarily mixed-conifer types in the Douglas-fir and grand fir zones, had substantial natural heterogeneity historically. Although these landscapes have received considerable logging pressure, the change from historical patterns caused by timber harvest may not be as pronounced as in very moist forests. We are not certain how birds most adapted to using these heterogeneous habitats have been affected by the current level of fragmentation of these landscapes caused thus far by timber harvesting, or if timber harvesting would compensate for changes from fire suppression, either in structure or extent. Most bird species that use Douglas-fir or mixed-conifer forest also use other forest types (Hutto and Young 1999). From the one study conducted in this forest type exclusively, three species (Red-breasted Nuthatch, Golden-crowned Kinglet, and Townsend’s Warbler) were negatively associated with more than one fragmentation index (Table 3), but we had classified two of these species as more associated with moist, continuous forests.

Similarly hard to interpret are the consequences of landscape changes in low-elevation dry forests. These forests are likely to have been the most affected by timber harvest, fire exclusion, and proximity to agricultural land and human development, but so many different changes have occurred on each piece of ground that there is no general landscape pattern that has been created. We speculate that low-elevation, dry savannah-like forests with many natural openings (e.g., ponderosa pine) that often are intermixed with grasslands would favor birds that exploit relatively open habitats, and that these birds are less likely to be negatively affected by the intrusion of openings caused by timber harvesting, as long as sufficient amounts of their required habitat elements are available (i.e., above a “habitat loss” threshold; Andrén 1994, Fahrig 1999). Birds associated with ponderosa pine and

many Douglas-fir cover types include Flammulated Owl, Lewis’ Woodpecker, White-headed Woodpecker, White-breasted Nuthatch, Cassin’s Vireo, and Chipping Sparrow. Chipping Sparrow had a positive association with fragmentation indices in two studies, but Cassin’s Vireo had mixed associations. In addition, it recently has been shown that Flammulated Owls are associated with open, edge habitats (Goggans 1986) and with old-growth ponderosa pine interspersed with grasslands at the large landscape scale (Wright 1996). However, in the current era of fire suppression, many low elevation dry forests now support increased tree density and canopy cover (Arno *et al.* 1997). The consequences of these changes in structure have not been adequately explored, nor have the consequences of human encroachment near these forests.

Patch size was important for some species in remnant patches of old-growth ponderosa pine (Aney 1984). This study, however, is the only one that has examined patch size for the vanishing habitats for which we are concerned, and no one has examined whether patch isolation influences early post-fire, aspen, old-growth ponderosa pine, or old-growth larch patch occupancy by birds. We believe that these issues are especially critical for birds that specialize on these habitats, given the trend of increasingly smaller and more isolated patches.

Three demographic studies (D. Evans *et al.*, unpubl. report; S. Hejl, unpubl. data; R. Sallabanks, unpubl. report) found little to no cowbird parasitism in areas fragmented by logging or in continuous forests. Most of these specific landscapes were far from human-added features with which cowbirds may be associated, but this needs further investigation. Overall, the impact of cowbirds on conifer forest birds in the north-central Rockies currently appears small relative to other factors. Parasitism rates, however, are likely to be high in those conifer forests near agricultural areas or residential development (not well studied), and if human-added features spread throughout conifer forests in the north-central Rockies, then we would expect Brown-headed Cowbird parasitism to increase as well.

There is fairly convincing evidence that assessing the effects of changes in forest landscapes for birds in the north-central Rockies, as elsewhere in the West, requires a different approach from the model developed from more static, fragmented landscapes in the East and Midwest in North America. More extensive forested areas in the East and Midwest may indeed have similar landscape conditions to those most prevalent in north-central Rockies forests, but most fragmentation studies in those regions have dealt with “remnant patches” (*sensu* Forman

and Godron 1986) in the middle of disturbed habitat. In contrast, the natural situation in the north-central Rockies is one of "disturbance patches" (sensu Forman and Godron 1986), such as early post-fire forests or timber harvest openings, in the middle of a less disturbed landscape matrix (Faaborg et al. 1995).

These differences in patterns and processes between regions within North America, and their concomitant differences in avian response, have been reviewed elsewhere. The relationships of increased abundance and species richness with forest fragment size were more pronounced for long-distance migrants and open-cup nesters in eastern and midwestern studies compared with residents or short-distance migrants (Faaborg et al. 1995). In northeastern and central hardwood forests, 72% of species showing area sensitivity in at least some studies were long-distance migrants, compared with 29% in western forests (Freemark et al. 1995). Studies in the north-central Rockies support the conclusion that resident species are equally or perhaps more likely to be negatively affected by fragmentation than migrants. The effect of increasing edge in eastern North America results in greater access of some nest predators into forests (e.g., Brittingham and Temple 1983, Robinson 1992), but this pattern does not necessarily hold in the landscapes of the north-central Rockies. Timber management (e.g., clearcuts) in western coniferous forests introduces few new predators to the biotic community (Marzluff and Restani 1999). In some landscapes of the north-central Rockies, red squirrels and some corvids are at least as abundant in uncut forest as in disturbed areas (Evans and Finch 1994). Thus, we would expect that predator response to changes in western coniferous forest landscapes, and the subsequent effects on nest success, may be better explained by something other than "edge effects." Predator dynamics within these forests have yet to be explored adequately.

Because habitat loss and habitat fragmentation are interdependent (Faaborg et al. 1995, Fahrig 1999), it is difficult to separate the possible consequences of habitat configuration from loss of habitat per se. In modeling thresholds of fragmentation effects, Andr n (1994) proposed that in landscapes with >30% suitable habitat, the amount of habitat was more important than its configuration. Only when suitable habitat was reduced to <30% did patch size and isolation begin to influence bird populations. Most of the studies in the north-central Rockies (and most throughout the West) generally occurred in landscapes with >30% forest cover. Ten landscapes in which nest success was studied by D. Evans et al. (unpubl. report) varied from 32–78% forest

cover, and the authors believed that they may have detected some fragmentation effects in stands at the low end of this range. Given the regional differences in areal extent of forest cover across North America and the types of changes to forests of the north-central Rockies that we describe, it is not surprising that forest size was a dominant influence in midwestern and eastern studies, whereas change of within-stand structure and loss of nest and foraging substrates may predominate in the north-central Rockies.

There are, however, instances when the model of patch size and isolation may be applicable to coniferous forests of the north-central Rockies—specifically for habitats that have become scarcer on the landscape. This includes lower elevation old-growth habitats, which have been heavily harvested and are now disjunct, although perhaps not surrounded by completely dissimilar habitat. Fire disturbance patches, which currently are in decline due to fire suppression, probably represent another example. From a landscape perspective, fire suppression and logging not only decrease potential habitat for old-growth specialists (e.g., Pileated Woodpecker) and post-fire specialists (e.g., Black-backed Woodpecker; Hutto 1995), but also further isolate those habitats, potentially decreasing the viability of populations of such species in the north-central Rockies. What is most important for these birds today is to restore the historical patterns and the processes that created the landscapes for which the birds evolved (Hejl et al. 1995, Hejl 2000).

When not suppressed, stand-replacement fires create well-defined fragments of early successional forest dominated by standing dead trees (Hutto 1995). This is the earliest and most ephemeral condition in post-fire succession. These sites provide nesting opportunities for many primary and secondary cavity nesters, and timber drillers are attracted by the abundant beetle larvae (Hutto 1995). In a literature review, Hutto (1995) noted 15 bird species found equally or more consistently in recently burned forests than in any other vegetation cover type in the northern Rocky Mountains, and some species were nearly restricted to such conditions (Hutto 1995, Hutto and Young 1999). The Black-backed Woodpecker, for example, has been designated a "sensitive species" in several regions by the U.S. Forest Service for precisely that reason. Other species that were most commonly found in burned forests include Three-toed Woodpecker, Hairy Woodpecker, Olive-sided Flycatcher, Mountain Bluebird, American Robin, and Cassin's Finch (Hutto 1995). Early post-fire patches are a naturally fragmented system, but decades of fire suppression have de-



creased the total area involved and increased the isolation of each burn (Baker 1994). Bird species restricted to such ephemeral, early post-fire patches would have to be adapted to quickly colonize new patches, but increasing isolation may place a strain on individuals finding new patches. In addition, post-fire salvage logging may diminish the suitability of some patches by reducing nest sites and food resources (Caton 1996, Hitchcox 1996, Saab and Dudley 1998).

Finally, BBS data may not be a useful tool for evaluating the effects of landscape changes on birds in these forests. We used BBS to examine regional trends, because we assumed that if landscape changes had greatly affected a species, we would see that reflected in regional trend information. We recognize that our interpretations of these data may be limited because BBS surveys take place on roads and therefore do not sample all landscape situations equally, may sample edge habitat although classified as "forest," do not sample many conifer forest birds well [55% of conifer birds in the north-central Rockies (noted here) and 50% in western North America (Hejl 1994) did not have reliable population trends], and are limited to the most recent 33 years. Indeed, of the 14 species most likely to be negatively affected by fragmentation according to community abundance studies (Table 3), BBS has significant positive trends for two species, indicating either that these species have not been negatively (or may even have been positively) affected by landscape changes in the past 33 years, or that BBS does not sample these birds or issues very well. Alternatively, BBS might be adequate for some of these species or issues, and the general lack of negative trends could indicate that many of these species have not been negatively affected by landscape changes during the past 33 years. We are concerned, however, about the 55% of the species that are not sampled well by BBS. Many of these species are among those most likely to be negatively affected by landscape changes associated with timber harvest and fire exclusion. In general, these species are difficult to study and would benefit from species-specific investigations.

## CONCLUSIONS

Overall, our understanding of the relationships between landscape changes and coniferous-forest birds in the north-central Rockies is rudimentary. We have a growing understanding of the landscape issues (current vs. historical patterns and processes), but only scattered in-

formation concerning how changes in these landscape patterns may have influenced bird populations, and then only during the breeding season. However, preliminary work suggests that fragmentation is not clearly affecting as many species as in other parts of North America. Differences from fragmentation issues in other regions are due to the kind and degree of fragmentation. In most north-central Rockies conifer forest landscapes, forests are interconnected and far from cowbird feeding sources or predators associated with human residences. Since the effects of some landscape changes in the north-central Rockies are likely to be less dramatic than those that have been documented in the East and Midwest, population responses of species may be subtle and difficult to measure. Large sample sizes are needed to determine if subtle effects are real and biologically significant enough to result in declining populations.

In the future, we need more studies on nesting success, survivorship, dispersal, predator ecology, and parasitism rates in relation to landscape patterns as well as within-stand changes. Research during the nonbreeding season also is needed. We offer our proposed consequences as hypotheses upon which to base future tests. Our greatest concerns are for those species that are associated with habitats that have changed the most, are vanishing, or are near added landscape features that cowbirds use. The loss of fires may be the single greatest continuing threat to birds in these landscapes, via the loss and isolation of critical habitat components (such as snags).

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