



Effects of fire on avian distributions and patterns of abundance over two vegetation types in southwest Montana : implications for managing fire for biodiversity
by Steven J Henderson

A thesis submitted in partial fulfillment Of the requirements for the degree of Master of Science in Biological Sciences
Montana State University
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Abstract:

Fire is the primary natural disturbance in many North American terrestrial ecosystems. However, human exclusion of fire over the past century in grassland and forest biomes has influenced natural fire regimes, successional trajectories, and vegetation patterns. Fire management in southwest Montana is an excellent example of attempting to mitigate effects of fire exclusion in a fire-adapted system, and manage native vertebrate diversity, through reintroducing fire in particular vegetation types. The mid-elevation zone of the Deerlodge National Forest in southwest Montana is characterized as a mosaic of 3 potential natural vegetation (PNV) types: dry upland meadow, dry conifer forest, and valley-bottom grassland. Fire management over this landscape has been influenced by this variation, as meadows have experienced prescribed burning since the early 1970's (following a period of fire exclusion) while fire has been excluded in forest vegetation over the past century. Prescribed burning in upland meadow PNV has commenced partly under the assumption that fire limits conifer-encroachment and maintains meadow patches through time, enhances habitat for early-seral species, and increases regional biodiversity. In this study, I addressed the following questions: 1.) How does fire influence landbird distributions, patterns of abundance, and diversity over 2 PNV types in southwest Montana? 2.) Do fire-associated or early-seral bird species occur over this landscape? 3.) How effective are current fire management practices for maintaining fire-associated or early-seral bird populations and regional avian diversity? I sampled abundance of 52 landbird species and vegetation structure over a postfire chronosequence in two PNV types (dry conifer forest and upland meadow) during the 1995-1996 bird breeding seasons. Sampling points (n = 148) were distributed over 37 stands, stratified by PNV type and time-since-fire (TSF) within a PNV type. TSF was the number of years since prescribed burning and high-severity wildfire in upland meadow and forest PNV, respectively. Distributions of 24 bird species were explained by PNV type irrespective of fire history, TSF only, or both variables. TSF explained variation in vegetation structure within both PNV types, and strong associations (+ or -) among bird abundance, TSF, and vegetation structure gradients emerged. Several bird species were early-postfire or late-seral associates within forest or meadow PNV; although nearly all early-postfire associates occurred in forests rather than meadows. Early-postfire forest bird communities were unique, however only a weak relationship between TSF and avian community composition was detected in meadows. Although prescribed burning in meadows is important for long-term persistence of this PNV type and its associated avifauna, I conclude that current fire management (prescribed burning in upland meadows while excluding fire in forests) is not adequate to maintain several fire-associated or early-seral bird species. In conjunction with reintroducing fire, identifying appropriate settings within landscapes to initiate or allow burning is a fundamental consideration, and these settings should vary according to resource management objectives. This study emphasizes the importance of high-severity forest fire for maintaining local populations of several bird species and regional biodiversity.

EFFECTS OF FIRE ON AVIAN DISTRIBUTIONS AND PATTERNS OF
ABUNDANCE OVER TWO VEGETATION TYPES IN SOUTHWEST MONTANA:
IMPLICATIONS FOR MANAGING FIRE FOR BIODIVERSITY

By

Steven J. Henderson

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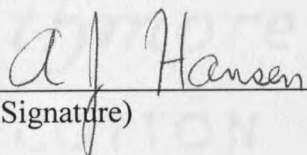
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Steven James Henderson

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Andrew J. Hansen

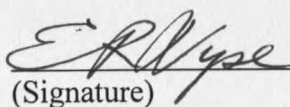


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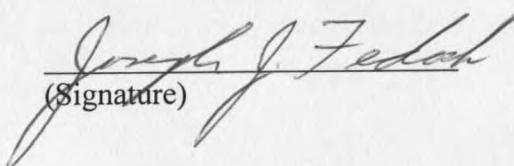


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Joseph J. Fedock



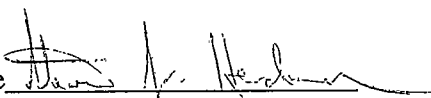
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ABSTRACT

Fire is the primary natural disturbance in many North American terrestrial ecosystems. However, human exclusion of fire over the past century in grassland and forest biomes has influenced natural fire regimes, successional trajectories, and vegetation patterns. Fire management in southwest Montana is an excellent example of attempting to mitigate effects of fire exclusion in a fire-adapted system, and manage native vertebrate diversity, through reintroducing fire in particular vegetation types. The mid-elevation zone of the Deerlodge National Forest in southwest Montana is characterized as a mosaic of 3 potential natural vegetation (PNV) types: dry upland meadow, dry conifer forest, and valley-bottom grassland. Fire management over this landscape has been influenced by this variation, as meadows have experienced prescribed burning since the early 1970's (following a period of fire exclusion) while fire has been excluded in forest vegetation over the past century. Prescribed burning in upland meadow PNV has commenced partly under the assumption that fire limits conifer-encroachment and maintains meadow patches through time, enhances habitat for early-seral species, and increases regional biodiversity. In this study, I addressed the following questions: 1.) How does fire influence landbird distributions, patterns of abundance, and diversity over 2 PNV types in southwest Montana? 2.) Do fire-associated or early-seral bird species occur over this landscape? 3.) How effective are current fire management practices for maintaining fire-associated or early-seral bird populations and regional avian diversity? I sampled abundance of 52 landbird species and vegetation structure over a postfire chronosequence in two PNV types (dry conifer forest and upland meadow) during the 1995-1996 bird breeding seasons. Sampling points ($n = 148$) were distributed over 37 stands, stratified by PNV type and time-since-fire (TSF) within a PNV type. TSF was the number of years since prescribed burning and high-severity wildfire in upland meadow and forest PNV, respectively. Distributions of 24 bird species were explained by PNV type irrespective of fire history, TSF only, or both variables. TSF explained variation in vegetation structure within both PNV types, and strong associations (+ or -) among bird abundance, TSF, and vegetation structure gradients emerged. Several bird species were early-postfire or late-seral associates within forest or meadow PNV; although nearly all early-postfire associates occurred in forests rather than meadows. Early-postfire forest bird communities were unique, however only a weak relationship between TSF and avian community composition was detected in meadows. Although prescribed burning in meadows is important for long-term persistence of this PNV type and its associated avifauna, I conclude that current fire management (prescribed burning in upland meadows while excluding fire in forests) is not adequate to maintain several fire-associated or early-seral bird species. In conjunction with reintroducing fire, identifying appropriate settings within landscapes to initiate or allow burning is a fundamental consideration, and these settings should vary according to resource management objectives. This study emphasizes the importance of high-severity forest fire for maintaining local populations of several bird species and regional biodiversity.

INTRODUCTION

Fire is the primary natural disturbance in many North American terrestrial systems (Ratz 1995, Whelan 1995). However, human exclusion of fire over the past century in grassland and forest biomes has profoundly influenced natural fire regimes, successional trajectories, and vegetation patterns (Baker 1992). A current challenge is to understand immediate and long-term effects of fire on ecosystem processes and apply this information to successfully reincorporate this disturbance type in fire-adapted regions (USDA and USDI 1995).

Reincorporating fire in temperate forest, grassland, and shrubland landscapes through prescribed burning and prescribed natural fire is emerging as a strategy to mitigate effects of fire exclusion and manage biodiversity in fire-adapted ecosystems throughout North America. The Federal Wildland Fire Policy (FWFP; USDA and USDI 1995) recognized wildland fire as a critical ecosystem process, and emphasized the necessity of reintroducing fire into natural systems on public lands, especially in areas where fire exclusion has altered biotic communities. Of the > 600 million acres of Federally-managed land, prescribed fire has treated approximately 5 million acres per year (Ward et al. 1993), although the majority (70%) of prescribed burning has occurred in the southeastern United States (Mutch and Cook 1996).

In association with reintroducing fire to manage native biodiversity in fire-adapted systems, identifying appropriate settings within landscapes to initiate or allow burning is an important consideration. Fire effects vary over landscapes as a function of variation

in vegetation and biophysical properties (Whelan 1995). Accordingly, how prescribed burning or natural fire influences biodiversity and species distribution patterns probably depend on where fire is placed or allowed in landscapes. For example, frequent, low-severity prescribed fires may be appropriate in valley-bottom grasslands, while more severe and less frequent prescribed fire may be required to maintain upland forest communities.

Fire management in southwest Montana is an excellent example of attempting to mitigate effects of fire exclusion in a fire-adapted system through reintroduction of fire. I suggest that consideration of landscape context is helpful in this system when reintroducing fire to manage for native biodiversity. The mid-elevation vegetation zone in this region (ca. 1585 - 2240 m) is naturally fragmented and characterized by dry upland meadows (often shrub-dominated) interspersed among an otherwise forested landscape (Figure 1). Lower elevations and alluvial valley bottoms typically support grassland vegetation. However, these vegetation types have experienced significant changes over the past century since European settlement (Gruell 1983a, 1983b). Fire exclusion policies and elimination of aboriginal ignitions have facilitated forest encroachment into grasslands and upland meadows that historically dominated the drier and more productive sites. The resulting successional patterns are probably atypical of those of pre-fire exclusion landscapes where fires limited establishment of woody vegetation (Gruell 1983a). Hence, it is likely that the area of native grassland, shrubland, and early-postfire forest habitats in southwest Montana has declined substantially over this time period. Consequently the Deerlodge National Forest (DNF) in southwest Montana is

experimenting with prescribed burning in upland meadows to maintain this vegetation type, manage native biodiversity, and accommodate species associated with early-seral vegetation. However, a policy of fire exclusion remains in place for forest vegetation.

Figure 2 provides a conceptual model of factors influencing vegetation structure over southwest Montana and illustrates how effects of fire initiation and fire exclusion on vegetation structure may vary across landscapes. Adapted from Kuchler (1964), three types of potential natural vegetation (PNV) are recognized in this landscape: dry conifer forest, upland meadow, and grassland. PNV refers to the most likely vegetation community type in absence of human disturbance such as fire exclusion. PNV is typically a product of interactions among climate, geomorphology, natural disturbance, and the biota. Traditional treatments of PNV are based on a coarse-scale vegetation classification system over the United States. However, I apply the concept here at a more local spatial scale, to major vegetation units within watersheds. The three PNV types I focused on were valley-bottom or alluvial grasslands, edaphically-controlled upland shrublands, and upland dry conifer forests. Importantly, a PNV type includes all seral stages along a successional trajectory. For example, the stem-initiation, stem-exclusion, understory reinitiation, and gap-phase seral stages (Oliver and Larson 1990) depicted in Figure 2 all exist within the forest PNV.

Landscape variation in southwest Montana has primarily been attributed to historic frequent fire impeding conifer colonization and establishment in upland meadows and valley grasslands from adjacent coniferous forest vegetation (e.g., Gruell et al. 1986). Also, wildfire influences stand structure within forest vegetation (Muir 1993). I

hypothesize that abiotic factors largely control broad distributions of these PNV types in southwest Montana, and that recent fire history influences structural characteristics within PNV types. For example, on a coarse-scale, patterns of forest/upland meadow vegetation may partially be explained by elevation and edaphic factors. However, structural characteristics within forest/upland meadow PNV may largely be a function of disturbance (fire) history.

Figure 2 also accounts for uncertainty in successional trajectories (dotted arrows). For example, several studies (Arno and Gruell 1983; Gruell 1983a, 1986) document rapid rates of conifer encroachment into grassland and upland meadows over the period of fire exclusion, and suggest that these stands would succeed toward forest in the absence of natural disturbance. This trajectory is attributed to disruption of the historic mean fire interval (MFI) of 35 - 40 years (Arno and Gruell 1983) at the forest/nonforest ecotone through fire exclusion. Contrarily, several upland meadow stands and grasslands have not experienced considerable rates of conifer invasion over the period of fire exclusion, suggesting that fire is not the only factor maintaining upland meadows and alluvial grasslands. Strong gradients in abiotic factors probably play an important role in vegetation patterns and, in some cases, primarily control rates of succession in southwest Montana (see Hansen and Rotella, In Press). Sindelar (1971) suggested that fire exclusion is not the primary determinant of Douglas-fir invasion of western Montana grasslands; its influence is instead controlled by the strength of interactions with other abiotic and biotic factors. For example, effects of fire exclusion on conifer invasion may be amplified in periods of unusually heavy precipitation, but negligible in average years.

Additionally, Arno and Gruell (1983) implied that upland meadow sites in southwest Montana probably supported more shrub (e.g., sagebrush, *Artemisia* spp.) cover than valley bottoms regardless of fire history, generally as a result of coarser soils at higher elevations relative to the alluvial deposits characteristic of valley bottoms. If soil texture and shrub cover follow an elevational gradient, so might rates of conifer invasion irrespective of fire history (see Gruell 1986 for mechanisms facilitating conifer encroachment into dry meadows). Overall, it appears that both fire history and biophysical properties interact to control broad distributions in PNV types and stand types, although the relative importance of each probably varies with geomorphic setting.

Based on Figure 2, the effectiveness of prescribed burning or prescribed natural fire (the practice of allowing natural ignitions to burn) for maintaining fire-adapted species or regional diversity probably depends on the biophysical setting in which fire occurs. For example, if some early-seral species or guilds are exclusively associated with early-postfire forest vegetation, it is unlikely that current practices of prescribed burning in upland meadows and fire suppression in forests accommodate those organisms. Conversely, if fire exclusion does result in meadow succession toward forest, this practice will probably limit early-seral meadow associates over short time periods, and late-seral meadow associates over longer periods. Fundamentally, understanding habitat-associations and how species and communities are patterned over these PNV and postfire stand types are important for evaluating effects of fire management on biodiversity.

Landbird populations and communities are appropriate organisms for measuring relative responses of multiple species to disturbances (such as fire) which directly

influence vegetation structure and spatial arrangement. Landbirds as a group represent a multitude of life-history strategies and numerous species can be monitored relatively simply (Hutto et al. 1993). Relationships among vegetation structure, floristics, and bird community attributes are well-documented (MacArthur and MacArthur 1961, James and Shugart 1970, Rotenberry 1985). More recently, landscape structure -- variation in vegetation and patch structure over relatively large spatial scales -- has also been demonstrated to influence avian demography and patterns of abundance (Pulliam and Danielson 1991, McGarigal and McComb 1995, Flather and Sauer 1996). As fire often influences floristic composition (Ament 1995), stand structure (Day 1972, Muir 1993) and landscape pattern (Romme 1982, Baker 1992, Turner et al. 1994), landbird community response may sufficiently indicate the effectiveness of ecosystem management prescriptions based on disturbance. Indeed, numerous additional biotic and abiotic factors (e.g., competition, Schoener 1974; climate, Rotenberry 1978) influence variation in bird community structure; however bird-habitat relationships are nonetheless important among multiple interacting factors. Additionally, effects of fire on avian population dynamics and distributions in western North America, and the associated implications of long-term fire exclusion in fire-adapted systems, have become serious management concerns (Hejl 1992, Hutto 1995, Madden 1996).

Central Questions

In this study I addressed 3 questions: 1) How does fire influence landbird distributions, patterns of abundance, and diversity over two PNV types in southwest

Montana? 2) Do fire-associated or early-seral bird species occur over this landscape? 3) How effective are current fire management practices -- which involve prescribed burning in upland meadow PNV and wildfire exclusion in forest PNV -- for maintaining fire-associated or early-seral bird populations and regional avian diversity over southwest Montana?

Research Approach

Although several studies have documented fire effects on avian populations and communities in North America, many have been based on a temporally-static design (i.e., a burned/unburned dichotomy; however see Taylor and Barmore 1980, Fox 1983, Engstrom et al. 1984, Huff et al. 1985, Apfelbaum and Haney 1986, Raphael et al. 1987, Breininger and Smith 1992). Of those that have examined postfire community succession and accounted for temporal change in avifauna, few have been embedded within a landscape context, which may be most relevant to ecosystem management. Since birds are vagile and avian life history parameters are accommodated or constrained over multiple spatial scales, it seems appropriate to evaluate effects of fire on bird communities within and among multiple vegetation or PNV types in landscapes. Accordingly, a new approach might examine the role of fire history (time since fire) on bird communities in multiple adjacent PNV types within landscapes, and determine how PNV and fire history interact to influence regional bird abundance and distributional patterns. The approach employed in this study was to sample landbird abundance, community composition, and vegetation structure along a postfire chronosequence over

one fire cycle in two PNV types (forest and upland meadow) depicted in Figure 2. To address central questions 1 and 2, I tested for effects of PNV and fire history on bird species distributions; compared avian abundances and community structure among fire history classes (stand types) within each PNV type; and developed multivariate bird-habitat association models which included the variables PNV and fire history.

METHODS

Study Area

The study area included the mid-elevation vegetation zone (ca. 1585 - 2240 m) across a 100,000 ha portion of the Deerlodge National Forest (Figures 1, 3). Most study sites occurred in the Tobacco Root and Highland mountain ranges, where mean annual precipitation is 32.6 cm and average annual temperatures range from -2.5 to 12.8 degrees C. Douglas-fir and lodgepole pine (*Pinus contorta* Dougl.) are the dominant tree species in this zone, with less frequent limber pine (*Pinus flexilis* James) in dry meadows at the lower forest limit (Figures 3 and 4). Meadows are most abundant near the valley-bottom treeline, but also occur to mid-elevations in the Douglas-fir zone. I speculate that interactions between soil, climate, and disturbance history explain their distributions. These meadows are often dominated by Idaho fescue (*Festuca idahoensis* Elmer) and big sagebrush (*Artemisia tridentata* Nutt.), depending on disturbance history and geomorphic site properties.

Although the fire regime of mid-elevation forests adjacent to meadows in this particular region has not explicitly been described, a mixed-severity regime can be reliably inferred from treatments by Arno (1980, 1996) and Fischer and Clayton (1983); also, personal observation supports this. In a mixed-severity regime characteristic of interior Douglas-fir forests, stand-replacement crown fires occurred periodically (Arno 1980), and low- medium intensity surface fires occur more frequently. Crown fires generally result in mortality of most live vegetation at a site, while low-medium intensity events usually kill trees in only the smallest size classes. In upland meadows and at the forest/meadow ecotone, fires historically burned frequently (MFI = 35 – 40 years; Arno and Gruell 1983) and fire severity was high, as nearly all vegetation is consumed in an average natural fire event (e.g., Brown 1995).

Experimental Design and Sampling Site Selection

I established a postfire chronosequence in each PNV type to detect long-term change in vegetation and avian community structure as functions of fire history over the study area. While it is difficult to document successional change over relatively large temporal scales, this synchronic sampling design ('space-for-time substitution', Pickett 1989) partly circumvents this by allowing simultaneous sampling of sites varying in time since disturbance (e.g., Billings 1938, Crocker and Major 1955, Olson 1958).

I selected 30 stands for intensive bird and vegetation sampling in 1995, and 9 additional stands in 1996. However, 2 stands selected in 1995 were excluded from the study after concluding they misrepresented the larger study area, and the total sample size

became 37 stands. I stratified sampling of stands by PNV type (dry-conifer forest, upland meadow) and time since fire class. See below for a description of stand aging.

In forest stand types, time since fire is specifically referenced to high-severity stand-replacement wildfire. However, it must be noted that multiple low-severity burns may occur within a return interval of two high-severity events in a given stand, and this may especially be the case in mixed-severity fire regimes characteristic of interior Douglas-fir forests (Arno 1980, Fisher and Clayton 1983). Time since severe fire was used in this study because stands experiencing or originating from such events were relatively easy to identify and spatial extent was less ambiguous. Also, although high-severity events within the study area were historically less frequent than forest underburns, they are nonetheless an important component of the fire regime (Arno 1980), and their relevance to contemporary forest management and avian conservation is particularly acute (Hutto 1995). In meadow stand types, fire refers specifically to prescribed burning conducted in the Spring.

Site selection was tentatively based on available fire distribution maps, burn prescriptions, fire history records, aerial photo interpretation, and personal communication with USDA Forest Service and USDI Bureau of Land Management personnel. I then validated potential stands through field reconnaissance. Candidate stands were ≥ 40.5 ha (100 acres) (in order to accommodate a minimum of 4 sampling points per stand under spatial constraints described below), usually within Douglas-fir or lodgepole pine habitat types (Pfister et al. 1977) and relatively undisturbed by timber harvesting. I originally discarded 7 stands that were either too small or intensively

logged. Site selection and number of replicates (n) per treatment were additionally constrained by the availability of wildfire and prescribed fire history records throughout the region, and accessibility to each site. Although I attempted to control for confounding factors such as topography and vegetation, selection of several sites was opportunistic. For example, the locations of selected meadow stands were determined by where prescribed burning had previously occurred regardless of geomorphic or prior disturbance properties. Table 1 illustrates the experimental design and stand type descriptions are as follows.

Forest: Early-postfire represents Douglas-fir/lodgepole pine stands experiencing high-severity fire within the past 22 years. High densities of standing-dead trees (snags), few live trees, and sparse overstory cover characterize these stands.

Forest: Mid-seral classifies Douglas-fir and/or lodgepole pine stands experiencing stand-replacement fire 55 - 75 years ago. These sites share the following attributes: 1) even-age distribution of live trees; 2) high live-tree density; 3) dense overstory cover; and 4) sparse understory cover. Many stands are lodgepole pine-dominated, although succession toward Douglas-fir dominance in the absence of disturbance is evidenced by young Douglas-fir trees occupying the understory. Also, adjacent cover types are often mature Douglas-fir forest and indicate the later successional stages of this stand type.

Forest: Mature/Gap-phase denotes relatively old forest sites experiencing gap-phase succession. Six stands (replicates) within this treatment share the following characteristics: 1) Douglas-fir comprises > 90% of overstory vegetation; 2) high overstory; 3) medium to high overstory cover (%); 4) multiple-age structure; 5) no

catastrophic disturbance < ca. 200 years; and 6) evidence of periodic low-intensity surface fires.

Upland Meadow defines relatively open stands interspersed amongst an otherwise densely-forested landscape. Meadows are grass/shrub dominated or co-dominated with conifers, and all sites are experiencing conifer invasion and establishment in varying degrees. Several stands support distinct patches of live old and young conifers. Hence, these sites are mosaics supporting substantial within-stand variation with respect to dominant plant species and vegetation structure. I further classified meadow stands by fire history into 3 broad categories: Early-postfire, mid-seral, and late seral (See Table 1 for time since fire). Fire-induced mortality of encroaching (young) and established (old) trees resulted in variable snag densities and multiple dbh-classes of snags, further adding to the complexity of this PNV type.

Bird Abundance Sampling

Field assistants and I conducted 420 and 350 point counts (Hutto et al. 1986) during the bird breeding seasons in 1995 and 1996, respectively, to estimate breeding bird abundance and species composition in each stand. The sampling periods were 30 May - 29 June 1995 and 3 - 29 June 1996. We sampled 30 and 37 stands in 1995 and 1996 respectively. Data from all stands were used in statistical analyses, and in stands that were sampled multiple years, bird abundance was averaged over both years. Three mid-seral forest, 1 late-seral forest, and 5 mature meadow stands were sampled only in 1996, while all others were sampled in both years. If year as a covariate accounted for variation

in relative bird abundance over the study area, then separate analyses by year or an integrated analysis incorporating year would probably be necessary to isolate effects of fire and stand type on bird communities. However, an exploratory analysis examining the effect of year on bird abundance performed on a subset of the data indicated that merging data collected in 1995 and 1996, and including data collected only 1996, was justified.

In each stand, four points were located along a transect established through the stand; points were spaced ≥ 200 meters apart and usually at least 100 meters from an edge. Transects often intersected the centerpoint of each stand, but were not positioned in randomly-selected directions. Stand size limitations combined with distance-to-edge and distance-between-points constraints usually dictated transect orientation and point placement. At each point, observers recorded: 1) the four-letter code for each bird species detected by sight or sound at a particular location; 2) the number of individuals detected by sight or sound at that location; 3) the estimated distance category (in meters) from the observer to the bird(s); 4) date; 5) time of day; 6) the point number; 7) temperature, wind, and cloud conditions; and 8) vegetation cover type. The first point count along a transect began soon after the dawn chorus (usually between 0600 - 0630), and each count lasted 10 minutes. Counts did not proceed beyond 1000. We sampled bird abundance at each point three times throughout the 1995 breeding season, and twice in 1996. I minimized observer error and sampling bias (Keppler and Scott 1981) through a rigorous pre-sampling training period emphasizing visual and aural bird identification, distance estimation, and abundance estimation. To additionally minimize sampling bias, sites were sampled by different observers whenever possible.

Stand Structure and Habitat Attribute Sampling

Time Since Fire

Forest Sites

In forest stand types, time since fire (TSF) was estimated primarily through three methods depending on the stand age class depicted in Table 1. Stands within the mid-seral class had previously been delineated and dated on a USDA Forest Service fire distribution map of burns occurring between ca. 1900 and 1945. I corroborated the recorded ages with field validation; this included coring 8 - 12 trees representing the largest diameter-class within a stand using an increment borer, and estimating the average age of the stand through growth-ring counts. All stands examined were within reasonable agreement (ca. \pm 10 yrs.) of their mapped ages, and retained as sampling sites.

Four early-postfire stands in this study burned in 1988, and were identified and sampled by Hutto (1995) in 1989 and 1990. One additional stand was identified from aerial photograph inspection, and its date of burn (1974) was determined from USDA records.

Although early-postfire and mid-seral forest stands were aged with considerable accuracy, the high-severity fire histories of late-seral stands were less clear due to a lack of information on disturbance history and stand initiation. I selected 6 stands that appeared to not have experienced catastrophic disturbance in the last 100 years, based on stand characteristics such as well-developed overstory, multi-age structure, and evidence of gap-phase succession (Oliver and Larson 1990). I originally examined Geographic

Information System (GIS) data to identify potential stands that were classified as mature, followed by aerial photograph interpretation of textural attributes of stand overstory. Each selected stand was field-validated and retained if it met the aforementioned stand attribute criteria. Rather than assume a reliable date since the last catastrophic event (if one occurred), I instead used the estimated average age of the two largest dbh-classes as an index, assuming this would at least indicate the minimum time since the last catastrophic disturbance. Between ten and sixteen Douglas-fir trees were cored in each stand and aged according to the number of growth rings counted. Fifty years were arbitrarily added to each estimated age, to account for a period of time (the stand-initiation phase) where lodgepole pine, rather than Douglas-fir, comprised the stand (e.g., Fischer and Clayton 1983). At best, this approach accounts for the potential structural condition of forest stands in the absence of high-severity disturbance over a time period relative to the two other younger stand types. Accordingly, time since fire of late-seral classes is not intended to represent an accurate time since the last wildfire; instead it is treated as an index value relative to the younger stand types for analyses purposes. Clearly, a rigorous fire history and stand age examination (e.g., Arno et al. 1995) would be most informative, but was not within the scope of this study.

Upland Meadow Sites

Time since prescribed burning in upland meadows was obtained from USDA Forest Service burn prescription records and correspondence with Forest Service personnel. However, as with forest sites, fire history of the mature meadow stand types

was less clear, and a fire history index was established for analysis purposes. Five mature meadows of unknown age were identified with aerial photographs, and subsequently field-examined. In each stand, 10 - 12 trees representing the two smallest dbh classes (trees that were considered to be "encroaching") were cored and aged through growth-ring counts. I assumed that these trees colonized and established in these sites sometime after the last fire event (e.g., Fischer and Clayton 1983). Large trees were not considered since they are more likely to survive multiple low- and medium-severity fire events characteristic of upland meadows (Habeck and Mutch 1973), and do not provide a meaningful index. All estimated tree ages within a stand were averaged, and this value represented the time since fire index in each stand. As with forest sites, TSF of late-seral classes is not intended to represent an accurate time since the last fire; instead it is treated as an index value relative to the younger stand types for analyses purposes.

Habitat and Vegetation Structure

Vegetation measurements followed Hansen et al. (1994). At each point along the transect (see Bird Abundance Sampling), four 10-m radius satellite plots were established around the point center in the four ordinal directions (Figure 5). Plot centers were located 20 meters from the point center. Field assistants and I measured habitat variables as follows, and these variables are summarized in Table 2.

General Point Description

At each point, we recorded latitude, longitude, elevation and UTM, determined from a GPS unit. We determined the slope (from a clinometer) and aspect (compass) at

five locations around the point (point center and plot centers). Also, we indicated whether a rock outcrop exists within 100 m of the point (to account for important habitat features that may influence the bird community -- e.g., Rock Wren) (Hutto 1994).

Overstory Cover

We estimated live overstory cover (%) with a spherical densiometer (Lemmon 1956) at 5 locations around each point: the point center and each plot center. At each location, we recorded densiometer readings while facing north, east, south, and west. All readings within a stand were averaged to obtain an overall overstory cover value.

Trees

We recorded the number of live trees by species by height class by diameter-at-breast-height (dbh) class in each 10-m radius plot. At 3 sites, a 30 - 60-m radius plot was additionally used if we felt that the 10-m radius plots did not account for observable tree occurrence.

Snags

Snag density (defined here as the number of standing dead trees of natural or burned origin) was measured within each 10-m radius plot. A 40 - 70-m radius plot was additionally used in 2 stands. We recorded the species, dbh class, and height class for each snag.

Understory Cover

We measured total understory cover (%) and several categories of understory cover in 32 0.25-m² plots per point (128 plots per stand), using the following cover classes: 0%, trace-5%, 6-25%, 26-50%, 51-75%, 76-95%, and 96-100%. We visually estimated the following, within both 0-0.5m and 0.5-1.0 m height classes: total live cover; shrub cover by species; graminoid cover; and forb cover. Additionally we recorded rock cover and conifer seedling (trees < 60 cm high and < 2 cm dbh) cover by species.

Statistical Analyses

Data Treatment

Bird Abundance

For each bird species in each stand, I estimated its mean abundance per area sampled by averaging the number of detections over the number of points per stand and number of sampling visits per stand. Abundance estimates were computed as the number of bird detections within 100 m of a point and exclude birds flying over and not observed occupying the stand. The abundance estimates used here represent relative indices rather than true densities. However, relative indices usually suffice for site comparisons (Verner 1985), although their accuracy probably varies with taxon, habitat variability, and season (Rotella and Ratti 1986). Due to non-independence of sampling points within a stand, abundance estimations at each point and visit were not treated as independent samples in

statistical analyses, but rather as subsamples averaged to form stand-level abundance indices. In addition to species abundance, average species richness (number of species) and total abundance (combined abundance of all bird species) were then calculated from these data.

Vegetation

Each understory variable was recorded by its coverage class. However for statistical analyses, class midpoints were used (Daubenmire 1959) as illustrated in Table 3. Tree and snag counts were converted to number of individuals per hectare. To quantify stand structural complexity (defined here as stand-level variation in tree diameter-classes), I computed Shannon's Index for live tree frequency among 7 diameter classes. Prior to computing this index, 0.001 was added to all tree density values to circumvent problems with the \ln transformation of zeros in the data set.

Diagnostics and Transformations

Prior to conducting linear statistical analyses, I conducted diagnostics for nonlinearity and heteroscedasticity between potential independent (X) and dependent (Y) variables (Neter et al. 1996). I visually inspected several bivariate X-Y plots to assess these possible violations of linear model assumptions. Due to the large number of variables in the dataset and numerous pairwise combinations of variables, I plotted abundance of each species, total bird abundance, and species richness against only Time Since Fire (considered one of the most important independent variables in this study) to determine whether transformations appeared necessary. Diagnostics of more pairwise X-

Y combinations may have been helpful, but it is difficult -- if not impossible -- to simultaneously optimize multiple transformations for multivariate statistical analyses, and there is usually no panacean transformation to comprehensively remedy a multivariate data set (Taper pers. comm.). I detected heteroscedasticity and/or nonlinearity within the data set, and reduced them by the following transformations: Where Y = abundance of each species, total abundance for all species, or species richness, the selected transformation (Y') was

$$Y' = \ln(Y + 1);$$

where X = Time Since Fire (TSF), the selected transformation (X') was

$$X' = X^{0.1}.$$

The latter transformation (X') was only implemented for TSF of forest sites. See Table 4 for a summary of data transformations and an account of which analyses were based on transformed data. Nonlinear or curvilinear models could have been tested; however the major purposes of my analyses were to identify underlying models and quantify correlation structure, rather than explicitly develop models representing the exact form of relationships between variables.

Effects of PNV and Fire History on Bird Species Distributions

I used logistic regression to model a binary response (present/absent) of 52 landbird species to PNV and fire history class (FIRE). Prior to conducting this analysis, all 37 stands were coded according to their PNV and fire history classes (see Table 1 for stand stratification criteria). I treated PNV as a categorical-nominal variable assuming

two levels (forest, meadow) and FIRE as categorical-ordinal represented by three fire history classes (early-postfire, mid-seral, and late-seral). Accordingly, each stand was classified as either early-postfire forest, mid-seral forest, late-seral forest, early-postfire meadow, mid-seral meadow, or late-seral meadow. A bird species was considered present in a stand if its abundance value was greater than zero.

For each species, a family of four competing models was examined for variables explaining variation in bird distributions. The model PNV included PNV and the intercept; FIRE included FIRE and the intercept; PNV + FIRE (full model) included PNV, FIRE, and the intercept; and NULL included the intercept only. Akaike's Information Criterion (AIC, Akaike 1973) was used as the model selection criterion (see Burnham and Anderson 1992 for a demonstration of AIC); that with the lowest AIC value was considered the best model within the family of models tested. However if AIC values for multiple competing models were within two units, I selected the most parsimonious model. All logistic regressions were performed using the SAS System, version 6.11 (SAS Institute, Inc. 1996).

For species showing distributions explained by either or both independent variables, I additionally report its frequency among PNV and fire history classes to establish stand type associations.

Avian Community Structure Between PNV Classes

In a preliminary exploratory analysis, I used clustering and multidimensional scaling algorithms to visually discern any apparent patterns in avian community structure

(defined here as the occurrence and relative abundance of all community members) between forest and meadow PNV types. If bird communities between the two PNV types were distinct, stand-level analyses of relationships among fire history, stand structure and bird abundance within PNV types may prove most informative and efficient if conducted within, rather than among, PNV types. This analysis was conducted with STATISTICA version 5.1 (StatSoft, Inc. 1997) software. Although my findings are presented in the Results section, it is important to note here that for each analysis technique described below, separate tests were conducted for each of the two PNV types based on the results of this analysis.

Bird Abundance Among Fire History Classes

I conducted Kruskal-Wallis Analysis of Variance (ANOVA) to test for effects of TSF on bird abundance within each PNV class. The independent variable TSF assumed three levels: early- postfire (7.5 - 21.5 and 0.5 - 6.5 years since fire in forest and meadow, respectively); mid-seral (55.5 - 77.5 and 8.5 - 12.5 years since fire); and late seral (ca. 215 - 350 and > 50 years since fire). See Table 1 for the number of replicates (n) per stand type. For species varying in abundance among stand types ($P \leq .10$), I conducted a post-hoc multiple range test to examine pairwise comparisons of bird abundance between stand types. I used $\alpha = .10$ as the critical value for multiple range testing since this nonparametric ANOVA is generally more conservative than its parametric counterpart.

Avian Community Structure Among Stand Types

I used clustering and multidimensional scaling to assess avian community similarity among stand types in each PNV class. Using STATISTICA (StatSoft, Inc. 1997), single-linkage squared Euclidean distances were calculated for each pair of stands from the bird frequency data set (presence/absence only) to generate a dendrogram of stand clusters ($n = 17$ and 20 stands for forest and meadow analyses, respectively). The resulting $n \times n$ matrix of pairwise distances was passed through a multidimensional scaling algorithm to produce a 2-dimensional map of stand relationships with respect to avian composition. I visually inspected these graphs to determine whether stands tend to cluster according to their stand type affiliations or whether no discernible pattern exists, indicating random distribution of birds among stand types (community overlap).

Multivariate Habitat Associations

Principal Components Analysis

Multivariate analysis is a logical approach to quantifying postfire community-level change (Prodon and Pons 1992), as it facilitates simultaneous interpretation of multiple factors influenced by fire, and how factor combinations influence community measurements. I conducted a bootstrap principal components analysis (PCA) to reduce the dimensionality of the vegetation data (Jackson 1993) and determine whether a fire history gradient explained significant variation among a set of habitat variables in each PNV type. Manifestation of a fire history gradient would allow for identifying significant habitat variables loading positively or negatively along the axis and avian response to this

multivariate ordination.

I developed a program in MathCad version 6.0 (MathSoft 1995) to perform the bootstrap PCA. The PCA was based on the correlation matrix computed for selected habitat variables; input variables were those hypothesized to vary with fire history and correlate with bird abundance. The program included a function for correcting for axis reflection (reversal), a common problem associated with bootstrap sampling in PCA applications (Mehlman et al. 1995). For forest stand types ($n = 17$, and 600 bootstrap samples), the PCA included 11 variables: TSFIRE, OVER, CLA, CL0, CL1-2, CL3-4, CL5+, TOT1+, DBHMEAN, SNAGTOT, and SHAN. The PCA for meadow stand types ($n = 20$, and 600 bootstrap samples) included 12 variables: TSFIRE, HERB1, ARTR1, GRS1, FRB1, HERB2, ARTR2, GRS2, FRB2, CLA-0, TOT1+, and SNAGTOT. 95% confidence intervals (CI) around eigenvalues and eigenvector coefficients were generated and used to determine axis significance and interpretation. If the lower CI limit of the eigenvalue was greater than 1, an axis was tentatively considered important. For axes with eigenvalues > 1 , I examined confidence intervals around each eigenvector coefficient for axis interpretation. If a CI overlapped zero, its respective variable was considered negligible in the axis. Other variables either loaded positively or negatively on the axis, determining their relative positions and influences along the axis gradient in PCA space.

PCA Linear Regression and Bivariate Correlations

Many multivariate bird-habitat modeling techniques model bird abundance as a

function of numerous independent habitat variables simultaneously (e.g., multiple regression). However, some inherent problems with this approach are: 1) models can become complex and less interpretable quickly; 2) degrees of freedom are lost as the number of independent variables (model parameters) increase; and 3) multicollinearity among independent variables necessitates omitting some variables to reduce redundancy and instability in the data matrix, and important information may be lost. An alternative approach is to first perform a principal components analysis on only the habitat data to reduce the number of significant variables while minimizing information loss, then proceed with assessing relationships between bird abundance and PC axes (also see McGarigal and McComb 1995). Using PC axes as independent variables in regression analysis offers an additional value: axes are orthogonal composites of habitat variables, and no multicollinearity exists within a family of PC axes (independent variables). Accordingly, for principal components determined to be significant in the previous analysis, I computed the vector of PC scores ($X \cdot$ eigenvector coefficient). For each bird species showing nonrandom patterns of abundance among stand types in the Kruskal-Wallis ANOVA, I conducted a multiple linear regression to quantify relationships between bird abundance and principal components axes within each PNV type. A family of competing regression models included each univariate model, multivariate model, and the null model (intercept only).

AIC was used in regression model selection, while least-squares estimates of fit (R^2 , R^2 -adj) were examined for model suitability. AIC is derived from the number of model parameters and the log likelihood function; AIC for multiple regression models

was computed as:

$$AIC = -2 \cdot \log_e(L) + 2 \cdot p$$

where p = number of parameters, $\log_e(L) =$

$$-N \cdot \left(\ln \left(\sqrt{2 \cdot \pi \cdot \frac{SSE}{N}} + 0.5 \right) \right),$$

N = total sample size, and SSE = Error Sum of Squares from the regression function (Taper pers. comm.).

In addition to regression analysis, I computed Spearman Rank Order Correlation coefficients for each bird abundance-habitat variable pair. This was done to permit interpretation of potential variation in species abundance not explained by principal components axes. Multiple linear regressions and Spearman Rank Order Correlations were performed in STATISTICA, version 5.1 (StatSoft, Inc. 1997); AIC computations were automated using the STATISTICA BASIC language (StatSoft, Inc. 1997).

RESULTS

Vegetation Structure

Forest Stands

Vegetation structure varied among stand types within forest PNV. See Table 5 for parameter estimates of vegetation variables and 95% confidence intervals. Early-postfire stands supported the highest snag density (SNAGTOT), density of regenerating trees (CLA), and low densities of live trees greater than 10 cm dbh. Mid-seral stands were

highest in total tree density, overstory cover (OVER), and densities of small to medium-sized trees (2 - 30 cm dbh). Mature forest supported the highest structural complexity (SHAN), mean dbh, and density of large trees (> 30 cm dbh).

Meadow Stands

See Table 6 for parameter estimates of vegetation variables and 95% confidence intervals in meadows. Although total herbaceous cover did not significantly vary among meadow sites, stand type and fire history particularly influenced shrub (SH) and big sagebrush (ARTR) cover in both understory height classes. Mean values for these variables were lowest in early-postfire and highest in mature meadows. Total snag density was highest in prescribe-burned meadows (early-postfire and mid-seral), and negligible in late-seral stands. Unexpectedly, prescribe-burned stands supported higher live tree densities than unburned meadows.

Effects of PNV and Fire History on Bird Species Distributions

I detected 52 landbird species over all stands in the study area. Life history attributes and scientific names of detected bird species are reported in Table 17. Of the 52 bird species modeled, 26 were nonrandomly distributed over the DNF landscape with respect to PNV and fire history (Table 7). The remaining 26 species tentatively appeared to be randomly distributed with respect to the two independent variables considered here (however, see Scope and Limitations in Discussion).

Incidences of 11, 2, and 13 species were explained by PNV alone, fire history

alone, and both PNV and fire history, respectively. Here $\underline{P} \leq .05$ and $\underline{P} \leq .10$ are considered significant and marginally significant, respectively. However one species showing variation in distribution with fire history only (Stellar's Jay) was an incidental occurrence; it was only detected in one stand over the sampling area. Selected models other than NULL based on AIC for 5 species (Blue Grouse, Cassin's Finch, Hermit Thrush, Stellar's Jay, and Western Tanager) are considered questionable, since $.10 < \underline{P} \leq .192$.

Table 8 illustrates stand type associations based on incidence for the 25 non-incidental species explained by logistic regression models other than NULL. Nine species were detected more frequently in meadows, while 4 were detected more frequently in forests, irrespective of fire history. For example, Green-tailed Towhee was primarily found in upland meadow habitats in this study, but fire history within this vegetation type did not appear to influence its distribution. The distributions of 11 non-incidental species were influenced by both PNV and fire history. For example, Brewer's Sparrow was detected only in mature meadows dominated by structurally-rich big sagebrush. Also, Three-toed Woodpecker occurred exclusively in early-postfire forest. Hairy Woodpecker was the only species successfully modeled by fire history alone, occurring significantly more frequently in the early-postfire condition within each of these PNV types.

Avian Community Similarity Between PNV Classes

Although I detected variation in community structure not explained by PNV alone, Figures 6a and 6b illustrate a strong relationship between PNV and avian community composition. As expected, each PNV type appeared somewhat distinct with respect to its resident bird community.

Bird Abundance Among Fire History Classes

Forest Stands

Of the 42 bird species detected in forest stand types, 17 showed nonrandom patterns of abundance among stand types (Table 9); total bird abundance and species richness also varied among stand types ($P \leq .10$). Several species attained their highest abundance in one stand type, and some were detected exclusively in one stand type. Notably, Hairy Woodpecker, Mountain Bluebird, Rock Wren, Townsend's Solitaire, and Three-toed Woodpecker were more abundant in early-postfire forest than in any other forest stand type. Three-toed Woodpecker and Rock Wren were detected exclusively in the early-postfire condition of this PNV type, while Mountain Bluebird was relatively restricted to this stand type. Additionally, Three-toed Woodpecker was absent from nearly all meadow stand types (including prescribe-burned stands), and Townsend's Solitaire and Mountain Bluebird occurred in meadows only in relatively low abundance. Total bird abundance was lowest in mid-seral forest stands, while species richness increased with time since fire.

Meadow Stands

Abundance of 11 species and species richness varied with time since fire ($P \leq .10$), while I detected no significant variation in abundance among stand types for 31 species and total bird abundance (Table 10). Stands experiencing prescribed fire (early postfire and mid-seral stand types) supported the highest species richness and abundance of 10 species: American Robin, Clark's Nutcracker, Cordilleran Flycatcher, Dusky Flycatcher, Hairy Woodpecker, Hermit Thrush, Mountain Chickadee, Red-breasted Nuthatch, Western Tanager, and Yellow-rumped Warbler. One species, Brewer's Sparrow, was most abundant and detected almost exclusively in mature meadows not experiencing recent fire.

Community Similarity Among Stand Types

This analysis suggested that early-postfire forest bird communities are unique with respect to species composition; however mid-seral and mature/old-growth communities did not appear to differ from each other (Figures 7a and 7b). In meadow stand types, only a weak association between species composition and stand type appeared. Figures 8a and 8b possibly suggest clustering (and hence, uniqueness) of late-seral stands with respect to species composition.

Multivariate Bird-Habitat Associations

Principal Components Analysis

Forest Stands

The principal components analysis resulted in two significant axes (Table 11) which explained 73.5 % cumulative variance in the selected habitat data. The first principal component (PC1), accounting for 49.9% variance, represented a time since fire and structural complexity gradient: time since fire, overstory cover, density of large trees, mean dbh, and Shannon's Index (structural complexity) all loaded positively on this axis. Snag density was also a significant variable, loading negatively. The second principal component (PC2), accounting for 23.6% variance, represented the mid-seral forest condition. Overstory cover, small-medium trees, and total tree density load positively, while structural complexity and large tree density load negatively. Stands representing the PC2 condition are usually well-stocked lodgepole pine stands approximately 75 years following stand-replacement fire.

Meadow Stands

Similar to the ordination results using forest habitat variables, the PCA extracted a fire history gradient in meadow stand types. One principal component was determined significant for the PCA conducted on selected habitat variables for meadow stands (Table 12). PC1 explained 27% of the variance and represents a time since fire and shrub (particularly big sagebrush) cover gradient. TSFIRE, ARTR1, ARTR2 load positively

while GRS2 and SNAGTOT load negatively on the axis. Variation in live tree density was not accounted for in this axis.

PCA Linear Regression and Bivariate Correlations

Forest Stands

The 17 species showing significant variation in abundance among forest stand types from the Kruskal-Wallis ANOVA were modeled. Significant regression models were selected for 13 bird species, where either PC1 or both PC1 and PC2 explained a significant amount of variation in abundance ($P < .10$). Table 13 reports the best model for each species based on AIC, the relationship between bird abundance and PC axes, and species response to fire based on the slope of each β -coefficient. Time since fire and structural complexity (PC1) alone accounted for variation in abundance of 6 species (Dark-eyed Junco, Gray Jay, Mountain Chickadee, Red-breasted Nuthatch, Ruby-crowned Kinglet, and Yellow-rumped Warbler); whereas the full model (PC1 + PC2) was selected for 7 species (Hairy Woodpecker, Hermit Thrush, Mountain Bluebird, Rock Wren, Townsend's Solitaire, Three-toed Woodpecker, and Western Tanager). The univariate model including only PC2 (mid-seral forest condition) was not selected for any species.

Four species did not vary in abundance with PC1 or PC2 in this analysis: Chipping Sparrow, Clark's Nutcracker, Common Raven, Red Crossbill; Total Bird Abundance and Species Richness were also randomly distributed along these axes. However, Spearman Rank Order Correlation coefficients (Table 14) indicate that

significant bivariate relationships between bird abundance and particular habitat variables may explain observed variation in abundance of these species not accounted for by the selected principal components. For example, although Chipping Sparrow abundance did not significantly correlate directly with TSFIRE nor with the explicit linear combination of variables represented in either PC axis, it did appear to increase with the density of large trees and structural complexity, or perhaps some other variable(s) correlated with these. Also, species richness positively correlated with structural complexity, time since fire, and significantly so with CL3-4.

The following five species showed a positive response to stand-replacement forest fire (i.e., abundance of these species correlates negatively with PC1, or PC1 and PC2): Dark-eyed Junco, Hairy Woodpecker, Mountain Bluebird, Rock Wren, Townsend's Solitaire, and Three-toed Woodpecker. Seven bird species increased in abundance with time since fire and structural complexity and appear negatively affected by high-severity fire: Gray Jay, Hermit Thrush, Mountain Chickadee, Red-breasted Nuthatch, Ruby-crowned Kinglet, Western Tanager, and Yellow-rumped Warbler.

Meadow Stands

Species richness and 11 species identified as responsive in abundance to fire history in the Kruskal-Wallis ANOVA were modeled in the regression analysis. Significant regression models were selected for 8 species and species richness, where time since fire and shrub cover (PC1) alone explained variation in abundance. Table 15 reports the best model for each dependent variable based on AIC, the relationship

between bird abundance and the principal components axis (PC1), and species responses to fire based on the slope of each β -coefficient. Three species, American Kestrel, Cordilleran Flycatcher, and Hermit Thrush, were not significantly influenced by the fire history gradient.

Six species and species richness appeared to respond positively to fire in meadows (i.e., abundance decreased with time since fire): Dusky Flycatcher, Hairy Woodpecker, Mountain Chickadee, Red-breasted Nuthatch, Western Tanager, and Yellow-rumped Warbler. The two species responding negatively to fire were Brewer's Sparrow and Clark's Nutcracker.

The NULL model was selected for American Kestrel, Cordilleran Flycatcher, and Hermit Thrush, indicating no significant association between abundance and the linear combination of variables represented in PC1. However bivariate correlations (Table 16) suggested a negative relationship between Cordilleran Flycatcher abundance and time since fire, but a positive relationship with the density of large trees. American Kestrel appears positively associated with herbaceous (grass and forb) cover, density of large trees, and snag density, although these relationships were not statistically significant. Based on these bivariate correlations and personal observation, relatively open savannahs characterized by sparse large trees and snags within grassland vegetation, may represent suitable habitat for American Kestrel. Hermit Thrush abundance responded negatively to time since fire, but positively to density of large trees.

DISCUSSION

Faunal assemblages are rarely random collections of individuals and species, but instead patterned according to differential life history strategies relative to ecosystem attributes or constraints (e.g., Diamond 1975, Lack 1976). Moreover, natural disturbance plays a profound role in influencing biological communities in general (Sousa 1984, Pickett and White 1985), and limiting bird populations in particular (Rotenberry et al. 1995).

Several authors have investigated postfire avian abundances and compositions in western forests and shrubsteppe habitats. Taylor and Barmore (1980) reported greatest bird abundance, biomass, and diversity in forest stands 5-29 years following fire in Yellowstone and Grand Teton National Parks. Here, canopy closure (ca. 25 years postfire) explained most of the decrease in avian abundance and species diversity over the postfire successional sequence. In the Sierra Nevada, Bock and Lynch (1970) detected greater species richness and biomass in burned coniferous forest relative to unburned sites. Hutto (1995) emphasized the uniqueness of early-postfire bird communities among forest cover types in the northern Rocky Mountains. Bird community compositions and relative abundances in early-postfire stands differed substantially from those of other forest stand types. Additionally, several species reached higher abundances in early-postfire habitats, and some species appeared restricted to burned conditions (e.g., Black-backed Woodpecker, Three-toed Woodpecker). In shrubsteppe, fire usually reduces shrub cover and stimulates graminoid productivity. Consequently, fire often reduces the

frequency and abundance of shrub-obligate species while favoring grass-nesting birds (e.g., Bock and Bock 1987, Petersen and Best 1987).

Avian compositions apparently reflect seral stage characteristics, and differential foraging and nesting opportunities following fire. Accordingly, population and community responses to fire vary with geographic location, pre-fire stand structure, and life-history attributes of species. For example, insectivorous species dominate early-postfire forest avian assemblages, probably responding to increased abundances of wood-boring, bark-dwelling and aerial insects following fire events (Hutto 1995). Also, fire particularly enhances habitat suitability for primary cavity nesters, secondary cavity nesters, and brush-users in forests (Bock and Lynch 1970, Taylor and Barmore 1980), and maintains grass-nesting species in shrubsteppe vegetation.

How Does Fire Influence Landbird Distributions, Patterns of Abundance, and Diversity over Two PNV Types in Southwest Montana?

The results presented in this study demonstrate the importance of potential natural vegetation and fire-influenced stand structure for avian distributions and patterns of abundance across the study area. For species occurrence explained by fire history, PNV, or both, these results are consistent with other studies demonstrating the importance of disturbance on stand structure and landscape composition, and concomitant effects on avian distributions and abundance. For example, Hansen et al. (1993) emphasized that forest bird community response to landscape perturbation is largely a function of post-disturbance habitat patterning and life history strategies of individual species.

Additionally, Knick and Rotenberry (1995) demonstrated how both local (stand structure) and landscape-level factors influenced site selection of breeding passerines in fragmented shrubsteppe vegetation. Importantly, these studies underscore the importance of examining habitat attributes and species response to disturbance over multiple spatial scales.

In this study, PNV appeared more significant in influencing avian distributions (presence/absence) than fire history for several species. Specifically, PNV irrespective of fire history explained the distributions of 11 species. Interestingly, most species for which distributions were explained by PNV, irrespective of fire history, were most frequent in meadows. For example, Vesper Sparrow, Green-tailed Towhee, Western Wood-pewee, American Kestrel, Dusky Flycatcher, and Dark-eyed Junco were detected more frequently in meadow stands; only Gray Jay and Common Yellowthroat were more associated with forests. However, Common Yellowthroat was detected in small, isolated, mesic patches within the forest matrix, and its occurrence in forests probably depends on the presence of this riparian component.

The distribution of only one species, Hairy Woodpecker, was explained by fire history alone. It would appear that this species is widely distributed with respect to PNV type, being generally found in both forest and meadow. However Hairy Woodpecker is distinctly snag-associated, occurring most frequently, and in greatest abundance, in the early-postfire condition within each of these PNV types.

The 12 species for which the full logistic regression model, including both PNV and fire history, explained incidence may be considered among the most narrowly-

distributed with respect to these two independent variables. Three-toed Woodpecker, for example, was relatively restricted to early-postfire forests with high snag density, Brewer's Sparrow occurred primarily in mature (unburned) meadows supporting relatively high sagebrush cover, and I detected Brown Creeper and Cooper's Hawk only in mature forest of high structural complexity.

Patterns of Bird Abundance Along Fire History Gradients

Strong associations among time since fire, vegetation structure, and bird abundance emerged from this analysis. The principal components analyses and subsequent linear regressions illustrate the influence of fire history and successional gradients on variation in vegetation structure and avian abundance over the study landscape. In forest stands, the abundance of 6 species responded positively to high-severity fire, while that of 7 species increased along the successional gradient. In meadows, 7 species responded positively to fire while 2 were negatively affected. However, the abundance of several bird species appeared neutral with respect to variation along the fire history gradient in either PNV type, but were correlated with one or more individual habitat variables (Tables 14, 16). This illustrates an important limitation to the multivariate approach taken in this study, whereby dimensionality in the habitat data was reduced prior to bird-habitat association modeling. Here, it appears that abundances of several species did not correlate with the specific linear combination of habitat variables generated in the principal components analysis, but instead were best explained directly by univariate techniques. For example, although Chipping Sparrow abundance in forests

appeared random with respect to the selected principal components axes, it positively correlated ($P \leq .05$) with CL3-4, CL5+, DBHMEAN, and SHAN in bivariate space. Also, Clark's Nutcracker showed a neutral response to either PC1 or PC2 in forests, but was positively associated with TSFIRE and CL3-4, and negatively with SNAGTOT. Clearly, although there are benefits to relating patterns of bird abundance to multivariate habitat gradients, it is important to additionally examine which independent variables individually account for variation in bird abundance.

The inability to detect variation in abundance of several meadow occupants along the prescribed fire history gradient is not inconsistent with other studies of shrubsteppe bird response to disturbance. Petersen and Best (1987) reported insensitivity of 3 sagebrush-obligates to a prescribed burn in Idaho, and the population responses of these species to prescribed fire was inconsistent with other reported habitat associations. The authors speculated that regenerating herbaceous cover following fire may have produced forage of sufficient quantity and quality to partially compensate for elimination of primary habitat (sagebrush). Also, uneven burning and partial-kill of sagebrush was reported in their study, and this has been demonstrated elsewhere (Best 1972, Wiens and Rotenberry 1985) to not eliminate shrub-obligate species. However, Bock and Bock (1987) reported a dramatic population decline by shrub-obligates to a fire causing 100% sagebrush mortality in a Montana shrubsteppe. These results suggest either a linear relationship between abundance of shrub-associated bird species and shrub cover, or response thresholds (e.g., the 'logarithmic response', Prodon and Lebreton 1981) where a decrease in abundance (and perhaps local extinction) accelerates below some critical

amount of this habitat feature. Alternatively, site fidelity may result in time lags in population response to fire (Temple and Wiens 1989). For example, Wiens and Rotenberry (1985) reported population stability for Brewer's Sparrow (a sagebrush-obligate, Braun et al. 1976, Reynolds and Trost 1981) for at least 2 years following habitat alteration. They attributed this to the strong returning tendency of this species to a breeding location despite structural and floristic changes in breeding habitat characteristics, and perhaps resulting in immediate compensation for low breeding productivity.

Based on the previous discussion, it appears that abundance patterns of several bird species along the prescribed fire gradient in this study are influenced by the completeness and severity of prescribed burning (e.g., Rotenberry and Wiens 1978), and accordingly a function of the structural legacy following prescribed burning. I observed no meadow patches experiencing complete, uniform burning, as evidenced by patchiness in vegetation structure and ground-scarring. Ryan (1990) emphasized the inherent variation in prescribed fire effects, simply resulting from quasi-complete burning of a site, spatial variation in fuels, vegetation, weather, and resultant fire behavior. Also, Prodon and Pons (1992) pointed out that bird communities may not respond to the combustion of a substantial proportion of canopy in controlled burning, as long as sufficient cover remains.

One species, Brewer's Sparrow, was adversely affected by sagebrush mortality by prescribed fire, and was detected nearly exclusively and in greatest abundance, in mature sagebrush-dominated meadows. Also, Petersen and Best (1987) documented Brewer's

Sparrow local population declines following prescribed fire in sagebrush vegetation.

These results emphasize the importance of mature meadows for local persistence of this regionally- and nationally-declining neotropical migrant species (Dobkin 1994, Sauer et al. 1997).

For 4 tree-nesting species detected in both PNV types, a contradiction regarding the effects of time since fire on abundance between forest and meadows appeared. For example, Yellow-rumped Warbler, Red-breasted Nuthatch, Western Tanager, and Mountain Chickadee responded negatively to fire in forests, but in meadows appeared most abundant in recently-burned sites. Bivariate correlations (Tables 14, 16) suggested some explanation for this phenomenon. In both PNV types, each species positively correlated with tree structure; and in meadows, live tree density was actually highest in early-postfire meadow stands (Table 5), indicating substantial large-tree persistence (or negligible mortality) following fire in these sites. Here, it is important to recognize that prescribed burning *per se* may not always directly influence the abundance of certain species, but a more direct correlate is the structural legacy that persists following prescribed burning, which is a function of pre-fire vegetation structure and fire severity. Also, recent burn prescriptions apparently targeted meadows considered more wooded (encroached) than others, accounting for higher residual tree densities in "early-postfire" meadows than selected mature sites.

Reduction of shrub cover and snag generation from prescribed burning in meadows were evident (Table 6), and these habitat attributes may be the most important variables to persistence of some species at the local scale. Several authors reported on the

