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INDIRECT EFFECTS OF FIRE SEVERITY ON AVIAN COMMUNITIES IN PONDEROSA PINE AND ASPEN FORESTS IN WESTERN NORTH AMERICA: A REVIEW

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INTRODUCTION

Fire is a highly dynamic process, annually affecting large expanses of western forests (Allen *et al.* 2002, Morgan *et al.* 2003, Schnoenagel *et al.* 2004, Westerling *et al.* 2006). Even large, severe wildfires create heterogeneous effects across the landscape, and scientists use burn severity classifications to infer fire effects on soil and vegetation, potential successional trajectories, and rates of ecosystem response following fire (Jain *et al.* 2004, Lentile *et al.* 2006). However, the ecological implications of severity are variable within and across ecosystems and definitions vary among user groups, complicating the broad-scale interpretation of severity. Severity assessments tend to be qualitative and often fail to specifically identify how each severity level affects overstory or understory vegetation components, soil, erosion potential, or other

habitat attributes (Lentile *et al.* 2006, Lentile *et al.* 2007).

Broad-scale burn severity assessments require remote measurement of surface properties that can be mechanistically related to ground measures of post-fire ecosystem condition and used to predict likely trajectories of vegetation change (Smith *et al.* 2007). Scientists use severity mapping for multiple objectives related to post-fire project planning and monitoring, and research exploring relationships among pre-fire, mid-fire, and post-fire characteristics and response. Lawyers and politicians use severity information as evidence in legal debates surrounding post-fire timber salvage or restoration activities (Lentile *et al.* 2006). Despite the accessibility of satellite data and the utility of severity mapping, Stephens and Ruth (2005) noted that the only wildland fire data recorded as late as 2004 on Forest Service lands were total area

burned, fire location, and the dominant vegetation types within the fire perimeter. Remotely sensed data provide managers the ability to answer many questions about immediate and long-term ecological change, particularly whether fire effects are less severe in areas where they applied fuels treatments. For this reason, Stephens and Ruth (2005) suggested that fire severity information (unchanged, low, moderate, and high) be recorded for all large forest fires. However, any determination of fuels treatment effectiveness must be placed in the context of the local fire regime.

While scientists and managers recognize fire severity as an important influence on forests and their fauna (see Brown and Smith 2000 and Smith 2000 for broad overviews), we have, until recently, lacked the tools to incorporate explicit fire severity information relative to animal responses to fire at broad spatial scales. However, two developments have increased our ability to map fire severity. First, satellite data (e.g., Landsat, Moderate Resolution Imaging Spectroradiometer, etc.) are more readily available. Secondly, the recent development of methods (e.g., spectral mixture analysis, and differenced normalized burn ratio) allow managers to map severity at high spatial resolution and across large spatial scales (>100 000 ha) (Lentile *et al.* 2006, Smith *et al.* 2007). There have been fewer than 20 papers published since Brown and Smith (2000) and Smith (2000) that contain explicit examination of indirect effects of severity on wildlife habitat. In a recent review of fire effects on avian communities, Saab and Powell (2005) emphasized the need for future studies to incorporate fire severity effects in their analyses. Multiple studies have since examined avian responses to fire severity within ponderosa pine (*Pinus ponderosa*) and aspen (*Populus tremuloides*) forests. The purpose of this paper is: (1) to outline vegetation responses to fire severity within

ponderosa pine and aspen forest systems, (2) to review our understanding of the ecological effects of fire severity on avian communities within ponderosa pine and aspen systems with an emphasis on papers incorporating spatially explicit fire severity data, and (3) to suggest future research foci that will enhance our understanding of fire severity effects on avian communities within ponderosa pine and aspen forest systems.

VEGETATION RESPONSES TO SEVERITY

Fire effects on vegetation vary with burn severity. Burn severity integrates active fire characteristics (e.g., fire intensity and rate of spread), the immediate post-fire effects (e.g., vegetation mortality and soil charring), and longer-term responses (e.g., vegetation regrowth and insect population increases) into the vegetation structure, composition, and phenology (Lentile *et al.* 2006). Because changes to aboveground vegetation directly affect wildlife habitat, we define burn severity as a measure of fire-induced changes to vegetation composition and structure. These changes include direct and indirect responses to fire. Direct responses include immediate results such as vegetation scorch, consumption, and mortality. Indirect responses include increased physiological stress, delayed mortality, reduced competition, increased sprouting or growth rates, compositional change or a combination of these factors. Burn severity can be inversely related to vegetation recovery (i.e., severely burned areas take more time to recover to pre-fire levels or function). However, it is important to emphasize that there is no fixed pre-fire vegetation condition that necessarily represents a target for post-fire vegetation return. Furthermore, burn severity and the additive effects of multiple fires influence vegetation composition, structure, and successional dynamics through time and

across multiple spatial scales (Keane *et al.* 1990).

Typically, managers and scientists use the concept of severity to characterize fire regimes as low, high, and mixed, yet it is difficult to exclusively associate ponderosa pine or aspen systems with any particular fire regime. Historically, observers most commonly associated ponderosa pine with a low severity, surface fire regime; however, many recent studies described ponderosa pine within the context of mixed-severity fire regimes (Brown *et al.* 1999, Brown and Smith 2000, Kaufmann *et al.* 2000, Fulé *et al.* 2003, Graham 2003, Lentile *et al.* 2005). Mixed-severity regimes are not necessarily a new type of fire behavior and effects, but likely represent an acknowledgement of the complexity of fire effects and environmental responses. These regimes include a matrix of individual fires that burn simultaneously or at different points in time and have both lethal and non-lethal components. These regimes leave some dead and some surviving vegetation in patches of various sizes and shapes. Mixed-severity fire regimes may be the result of fine-scale, topographically-influenced differences in vegetation and fuel moisture that cause low- and high-severity fires to burn in proximity (Fulé *et al.* 2003). For example, when fires burning in dry coniferous forests reach moist coniferous forests, transitions in fire severity might occur due to changes in aspect, slope, or relative humidity. Therefore, the mixed-severity fire regime seems appropriate to apply to fire histories in ponderosa pine and in aspen forest systems (Agee 1998, 2005; Kaufmann *et al.* 2000).

Burn severity assessments provide a description of fire effects and relative measures of post-fire ecosystem change (Morgan *et al.* 2001, Jain *et al.* 2004, Lentile *et al.* 2006) within a single fire complex. Scientists often express burn severity qualitatively in terms of the post-fire appearance of vegetation, litter,

and soil using broad discrete classes of unchanged (no detectable change), low, moderate, and high (most extreme change). Scientists can quantify burn severity by measuring soil characteristics (e.g., char depth, organic matter loss, ash cover, and soil water infiltration rates; DeBano *et al.* 1998, Lewis *et al.* 2006, Lewis *et al.* 2008), tree mortality, canopy scorch, and change in vegetation distribution, abundance and structure (Turner *et al.* 1999, Morgan *et al.* 2001, Cocks *et al.* 2005, Keyser *et al.* 2006, Lentile *et al.* 2007). Lentile *et al.* (2005) mapped a mixed-severity wildland fire in Black Hills forests as having 18 %, 53 %, and 29 % of the burned area as low, moderate, and high severity, respectively. Within this fire, they defined low severity as areas with <25 % canopy scorch and 30 % groundcover consumption; moderate severity as areas with >25 % canopy scorch and 30 % to 70 % residual groundcover, and high severity areas had 100 % canopy scorch and >70 % groundcover consumption.

Scientists commonly use low, moderate, and high categories of burn severity to describe fire effects in ponderosa pine forests; however, there are no consistent descriptions for fire effects in aspen. Some studies describe three categories (e.g., Lentile *et al.* 2005), while others describe fires simply as low or high severity, or burned and unburned. Bartos and Mueggler (1981) described <20 % litter and duff consumption as low severity, 21 % to 80 % consumption and extensive mortality of understory vegetation as moderately burned, and >81 % consumption and complete understory vegetation mortality as severely burned. In general, many studies fail to define or describe metrics of fire severity, and merely report the proportion of the landscape mapped at a given severity. For this reason, it is often unclear what particular type of change or response researchers expect following fire.

In general, areas affected by different burn severity can function and respond differently

over time following fire. Less severely burned areas are likely to be more similar to pre-fire condition and function within a few years post-fire, while more severely burned areas may follow a different trajectory. In densely forested areas, severe fire may result in a complete cover type conversion, while more open canopy conditions may be created in moderately burned areas. Three years after a fire, Lentile *et al.* (2005) described tree mortality and changes in average tree size and basal area in areas of different severity: 21 %, 52 %, and 100 % post-fire tree mortality for low, moderate, and high severity, respectively. Live tree size increased and basal area remained relatively high ($\sim 29 \text{ m}^2 \text{ ha}^{-1}$ reduced to $23 \text{ m}^2 \text{ ha}^{-1}$) in low severity areas as fire killed smaller trees. However, in moderately burned areas, fire killed both small and large trees and reduced tree basal areas ($\sim 28 \text{ m}^2 \text{ ha}^{-1}$ reduced to $13 \text{ m}^2 \text{ ha}^{-1}$). Understory herbaceous cover was relatively unchanged in less severely burned areas, while the moderate to high severity areas had decreased cover with increasing severity. Understory and canopy cover conditions were most similar to pre-fire conditions in less severely burned areas, while opportunities for seedling establishment and the development of a dense, multi-aged forest were greater in moderately burned areas. In severely burned areas, they found two possible outcomes: in small openings created by high severity fire adjacent to surviving trees ($< 200 \text{ m}$), dense, even-aged forest structure was likely to develop; whereas, in larger openings, low seed availability and harsh environmental conditions limited seedling establishment and shrubs or grassland conditions were likely to develop (Lentile *et al.* 2005). Two years after this same fire, Bonnet *et al.* (2005) found the highest ponderosa pine seedling densities within severely burned patches near the edges of the unburned forest canopy. They found peak seedling densities ($\sim 1150 \text{ seedling ha}^{-1}$) at 12 m from the unburned edge, while < 100

seedlings ha^{-1} were found between 40 m and 180 m from an unburned edge (Bonnet *et al.* 2005). Although severely burned areas may function very differently than the pre-fire environment, these areas may provide unique habitat or structural components (i.e., high snag density, low tree canopy cover, high woody debris on the forest floor, many early successional plant species, etc.) that may be valuable to wildlife.

Historically, profuse post-fire regeneration via asexual reproduction was responsible for perpetuating aspen in many areas in the intermountain west (Campbell and Bartos 2001). Four years after a large wildfire in the South Dakota Black Hills, Keyser *et al.* (2005) found that the area occupied by individual aspen clones did not increase; however, they counted twice as many suckers in severely burned areas as in unburned clones. Additionally, they observed 67 % more suckers in areas burned by high severity than in low severity fire (Keyser *et al.* 2005). Brown and Bartos (2004) described burn severity effects on first-year aspen regeneration following six wildfires in South Dakota, Colorado, and Utah, including the aforementioned study. In this study, high severity sites most commonly produced the lowest suckering response, while low severity sites produced the greatest amount of aspen regeneration. Unburned sites generally produced fewer suckers than severely burned sites unless fires were severe enough to kill the aspen roots (Brown and Bartos 2004). This apparent contrast in results may be the result of different methodological approaches in terms of how each study defined plot size, burn severity characterizations, or the timing of the assessments. Clearly, vegetation change in the post-fire environment is highly dynamic.

The role of fire in adjacent vegetation types may regulate the extent and function of aspen forests (Romme *et al.* 2001). In mid-elevation ponderosa pine forests in Colorado, fires historically burned every 5 yr to 15 yr and

killed some trees in all size and age classes, ultimately reducing seed production and conifer establishment (Romme *et al.* 2001). Frequent fire and the reduction of conifer densities created opportunities for aspen to establish via asexual reproduction in open canopy, post-fire conditions. At higher elevations with longer fire intervals (~150 yr), conifer seed sources remained intact and aspen stands were successional. While conifers successfully out-compete aspen in a non-fire situation, after fires occur, aspen may regenerate in a pure stand due to extensive root suckering when the main trunk of the aspen is destroyed. In general, aspen are incapable of producing seedlings under a coniferous canopy as successful sexual reproduction requires a rare window of opportunity for seeds to germinate in the open under moist conditions on bare mineral soil. Extensive aspen seedling establishment occurred following the 1988 fires in Yellowstone; however, heavy elk browsing and adverse microclimatic conditions reduced the densities in most areas (Romme *et al.* 1995).

Forest floor consumption by fire is an important determinant of post-fire vegetation as it controls the amount and distribution of favorable germination and sprouting conditions across the seedbed. Two years following wildfire in ponderosa pine forests in Arizona, Laughlin *et al.* (2004) recorded a lower number of plant species in severely burned areas. They correlated this lower species richness with significant duff consumption. On sites where managers allowed frequent, low severity fires to burn, annual and biennial forbs were more abundant in the understory as compared to sites where managers excluded fires. On fire-excluded sites, Laughlin *et al.* (2004) observed more fire-intolerant tree species and exotic herbaceous plants. In a variety of forest types on low and moderately burned sites, Lentile *et al.* (2007) reported that organic material covered >30 % of the soil surface immediately

post-fire. One year later, the proportion of area covered by understory vegetation averaged ≥ 10 %. High severity burn sites had more exposed soil and less organic matter on the forest floor than less severely burned sites. In general, low burn severity areas showed the highest variability in understory plant response and high severity burns had the lowest. The variety of post-fire microsites on the landscape, including some unburned, some with charred organic cover on the soil, and some with bare soil, likely created conditions for many different plant species to survive, regrow, or establish from seed (Lentile *et al.* 2007). More severe fire resulted in a greater loss of organic matter on the surface or in the soil. Combustion of organic matter, the primary source of most available nitrogen, causes rapid volatilization of nitrogen; therefore, total and available soil nitrogen concentrations can increase, decrease, or stay the same following fire (Wells *et al.* 1979, DeBano *et al.* 1998, Ice *et al.* 2004) with no clear patterns established by severity.

Burn severity influences plant injury and mortality and the rate of reestablishment of resprouting species (Lyon and Stickney 1976, DeBano *et al.* 1998). Fire alters canopy and seedbed conditions; whether these conditions are favorable depends upon the characteristics of the plant species on the site, their susceptibility to fire, and the means by which they respond after fire (Mutch 1970, Lyon and Stickney 1976, Anderson and Romme 1991, Turner *et al.* 1998). The length of time that a seed environment retains conditions that are conducive to plant establishment determines the number of post-fire years in which seeding establishment of a particular species can occur (Wagle and Kitchen 1972, Shearer and Stickney 1991, Turner *et al.* 1998). In a long-term study of aspen community response to prescribed fire, understory biomass production (reported as dry weight) of forbs, grasses, and shrubs was initially lowest in severely burned areas. However, by the second year following

fire, overall production was ~66 % higher than pre-burn levels. By the third post-fire year, understory production exceeded pre-burn levels by 12 % on low-severity sites, 42 % on moderate-severity sites, and 52 % on high severity burned sites (Bartos and Mueggler 1981). Twelve years post-fire, understory production was 23 %, 42 %, and 46 % greater on sites burned at low, moderate, and high severities, respectively, compared to pre-burn levels. In the third year post-fire, aspen production was highest on the high-severity sites, although much lower than pre-burn levels. By 12 years post-fire, aspen production was lowest on the high severity sites; however, Bartos *et al.* (1994) attributed the decrease to heavy ungulate browsing. Plant regeneration may occur from on- or off-site seeds sources, or from deeply buried and protected root structures.

Although ponderosa pine and aspen are two of the most widely distributed tree species in the west, researchers have made many generalizations about their current status, mechanisms responsible for post-settlement change, and potential restoration techniques (Shinneman and Baker 1997, Baker and Ehle 2001, Bartos 2001, Campbell and Bartos 2001, Romme *et al.* 2001). Dendrochronological studies, historical records, and photos that document changes in western landscapes indicate that ponderosa pine densities, spatial patterns, and tree sizes are currently quite different from those of pre-settlement times (Allen *et al.* 2002, Fulé *et al.* 2002, Brown and Cook 2006). Aspen presence has declined by 60 % to 90 % since the late 1800s in some parts of the west (Kay 1997). Nearly one hundred years of fire exclusion has produced a more homogenous forest structure in most ponderosa pine forests with increased tree densities and greater duff accumulations, and a concomitant increase in burn severity (Covington and Moore 1994, Covington *et al.* 1997). Many aspen stands regenerated

following fires that occurred over a century ago and have not since regenerated. In some stands, aspen has been replaced by more shade-tolerant conifers (Keyser *et al.* 2005). Managers must recognize that ponderosa pine and aspen range across a broad geographical extent and, within the context of different fire regimes and burn severity effects, there is high variation in local biotic and abiotic factors. Therefore, no single or simple prescription is likely to restore these ecosystems given the complexity of ecological and social conditions that influence current management. Although several studies attempted to identify unifying trends in burn severity across ecosystems (e.g., Lentile *et al.* 2007, Hudak *et al.* 2007), it appears that standardization remains a challenge. Post-fire processes occur in a dynamic landscape that contains patches of different types of vegetation in various stages of succession. The diversity of habitats within the landscape may ultimately contribute to the diversity of the associated animal community (Tews *et al.* 2004).

INDIRECT EFFECTS OF SEVERITY ON AVIAN COMMUNITIES

Reproduction

Variations in fire severity can influence the demographic patterns of birds nesting within the landscape. For instance, Vierling *et al.* (2008) observed variable woodpecker reproduction in a mixed ponderosa pine and aspen forest system in the Black Hills during the first four years after a mixed severity fire. They reported that reproductive success (i.e., the number of nests that successfully fledge at least one young) of black-backed woodpeckers (*Picoides arcticus*), northern flickers (*Colaptes auratus*), and red-headed woodpeckers (*Melanerpes erythrocephalus*) differed among burn severities. Reproductive success for these species was high (78 %) in sites dominated by

high severity compared to the reproductive success (43 %) of those species in areas dominated by low severity (Vierling *et al.* 2008).

Habitat suitability can change as post-fire succession occurs. Two studies on avian communities in post-burn landscapes (Saab and Vierling 2001, Saab *et al.* 2004) suggested that recent, stand-replacing burns support high rates of avian reproduction primarily through adverse effects on potential nest cavity predators such as sciurids (e.g., squirrels and chipmunks). Immediately following a large stand-replacing fire, sciurids are rare in the landscape due to the lack of food and the lack of vegetative cover (Fisher and Wilkinson 2005). However, small mammal densities increase as new and recovering vegetation provides suitable food and cover (Fisher and Wilkinson 2005). This has important implications for avian reproduction in burned environments because predation on nestlings is a major, negative factor influencing the reproductive success for all birds (Wilcove 1985, Martin and Li 1992) and for birds nesting in burned habitats (Saab and Vierling 2001). Vierling *et al.* (2008) noted that reproductive success decreased in the first three years following fire, and they attributed the decline to increasing nest predation rates. This result is consistent with the hypothesis put forth by Saab and Vierling (2001) that recently burned habitats decline in reproductive quality (i.e., nest success) as potential nest predators colonize the landscape. However, Gentry and Vierling (2007) found that the reproductive quality of burned habitats may remain high even decades after a fire. In their study, reproductive success was 90 % in >20 yr old burn sites and the density of potential nest predators (weasels, squirrels, and chipmunks) was low compared to densities in adjacent unburned forests. This suggests that post-fire patterns of nest predator colonization and its effect on bird reproduction require further study.

Breeding Bird Community Composition

Post-fire succession is also likely to influence the breeding bird community, and several studies have addressed the early colonization of burned habitats relative to patterns of severity. In general, every community will have species that benefit from fires and species that do not (Kotliar *et al.* 2002). Smucker *et al.* (2005) explored the relationships between breeding bird community composition and fire severity in ponderosa pine and mixed conifer forests in Montana. They found that severity influenced species-specific density responses to fire. For instance, western tanagers (*Piranga ludoviciana*) glean insects off of the foliage and their densities were higher in burned patches (0.52 ± 0.05 individuals per 100 m² plot) than in unburned patches (0.44 ± 0.04 individuals per 100 m² plot; Smucker *et al.* 2005). However, density patterns became clearer from an ecological perspective when the researchers included severity in the analysis; densities were highest in low severity patches where some foliage was unchanged by fire. Alternatively, densities of western tanagers were lower in high severity patches, presumably due to the lack of foliage as a result of high severity fire effects. Low severity effects were primarily responsible for the positive influence of fire on western tanager densities. Low severity fires can increase nutrient availability for trees and shrubs (Turner *et al.* 1999). Therefore, the increase in tanagers following the low severity fire was likely due to an indirect increase in insect abundance caused by this increase in plant productivity.

The amount of time lapsed since fire burned an area also influences avian communities (Smucker *et al.* 2005). Smucker *et al.* (2005) stated that northern flickers (*Colaptes auratus*) did not show a positive response until three years after the fire. They noted that they would have missed this response had they surveyed the birds for only

one or two years post-fire. Although Smucker *et al.* (2005) did not comment on the reason for this delayed response, other studies have noted that colonization of burned habitats by bird species may be dependent in part on the landscape context of the burn, the size of the burn, the availability of food, post-fire salvage logging, fire severity, or a combination of these factors (Saab *et al.* 2005).

Smucker *et al.* (2005) also noted that fire severity effects on non-cavity nesting species varied with the amount of time since the fire. For instance, they noted that some species such as pine siskins (*Carduelis pinus*) peaked in the first year after the fire and declined thereafter. Smucker *et al.* (2005) hypothesized that short term increases in the availability of seeds were responsible for the pattern they observed in pine siskins and other seed-eating species. Due to the variability in temporal responses to fire severity by different species, Smucker *et al.* (2005) cautioned that pooling data across years might potentially mask important temporal variation in avian responses. The temporal responses of flickers and siskins illustrate the potential issues associated with pooling data. For instance, pooling data across multiple years for siskins would have masked the strong response that siskins showed in the first year after the fire. Likewise, pooling data for northern flickers for the first three years following the fire would mask the fact that researchers did not detect this species regularly until the third year following the fire.

Kotliar *et al.* (2007) examined avian community responses to fire severity in ponderosa pine using data collected before and two years after the Cerro Grande Fire in New Mexico. They found that species richness did not differ between pre-burn and post-burn environments, but that severity partially influenced community composition. Pre-burn and post-burn community similarity (i.e., the number of species occurring in both pre-burn and post-burn surveys within a site) was ~70

% to 80 % in unburned, low, and moderate severity sites. However, community similarity was ~55 % when comparing pre-burn vs. post-burn bird communities in high severity sites. Thus, they observed different bird species in the post-fire environment than in the pre-burn environment in high severity sites, but the overall species richness did not differ in these high severity sites. Kotliar *et al.* (2007) noted that ecosystem restoration programs might assume that severe fires in southwestern ponderosa pine forests will have largely negative effects on the avifauna of the region, but that their data did not support that assumption.

Nest and Roost Site Selection

Vierling and Lentile (2006) found that fire severity within aspen woodlands is an important determinant of nest-site selection for some species. For instance, red-headed woodpeckers are aerial flycatchers that utilize burned habitats in the eastern United States (Smith *et al.* 2000). Red-headed woodpeckers select aspen stands that burned under high severity rather than adjacent ponderosa pine stands that burned under high severity. Vierling and Lentile (2006) suggested that red-headed woodpecker nest site selection was due to the creation of suitable nesting and foraging habitat. High severity fires burned the understory and overstory sufficiently to allow aspen suckers and snowberry (*Symphoricarpos* spp.) to grow, which increased insect productivity in these aspen forests (Rumble and Anderson 1996). In comparison, the adjacent ponderosa pine stands that burned under high severity had similar numbers of snags (Lentile 2004), but lacked the primary productivity necessary to support insect activity. In addition, Smith *et al.* (2000) noted that red-headed woodpeckers require snags in which to nest, and snags were abundant in the high severity sites (Lentile 2004). Snags used

for nesting were farther from green forest (456.9 m \pm 66 m) than paired random sites (317.6 m \pm 60.8; Vierling and Lentile 2006). The location of the nests relative to green forest might have been driven by the lack of small sciurid predators in the high severity fire sites (Fisher and Wilkinson 2005). Nest-site selection is a dynamic process and researchers hypothesize that the risk of predation is one of the major factors influencing nest-site placement (Martin 1993). Therefore, we would expect nest-site selection to change as vegetation patterns change following fire.

Other cavity nesting species that inhabit ponderosa pine forests follow similar patterns in nest site selection. Vierling *et al.* (2008) examined nest site selection by northern flickers and hairy woodpeckers (*Picoides villosus*) in burned ponderosa pine in the first four years following a mixed severity fire. They found that these two species shared the best predictors of habitat selection: distance from an unburned edge, a high proportion of high severity fire within a 1 km radius, and relatively large diameter snags (e.g., >26 cm dbh) in which to nest. Vierling *et al.* (2008) suggested that the mechanism influencing nest-site selection of these two species was similar to the mechanism associated with the red-headed woodpecker nest-site selection; selection of nest sites occurred in areas farther from green forest and in regions dominated by high severity. This absence of adequate cover or food may influence the abundance of mammals that may act as nest predators.

Fire severity may affect movement patterns and roost use of avian species. Covert-Bratland *et al.* (2006, 2007) studied hairy woodpecker responses to fire severity in ponderosa pine forests in Arizona during the winter season. Covert-Bratland *et al.* (2007) radio-marked nine hairy woodpeckers and recorded the use and characteristics of 12 winter roosts. They found that roost trees were larger in diameter than random trees in the

study site and larger than other trees found within the same fire severity classes. Additionally, they found that fire created 67 % of the roost snags. Covert-Bratland *et al.* (2006) noted that hairy woodpeckers had higher densities in high severity sites; high beetle (a prey resource for these birds) densities within those sites in the first 2 yr to 3 yr following fire were a likely reason for this. Insect density also influenced woodpecker home range sizes, which decreased with increasing insect densities (Covert-Bratland *et al.* 2006). Covert-Bratland *et al.* (2006) noted that post-fire logging of snags in the first three years following high severity sites might decrease important winter foraging resources for hairy woodpeckers.

FUTURE DIRECTIONS

We focused this review upon indirect effects of fire severity in ponderosa pine and aspen forests on avian communities, and our discussion below is limited to these ecosystems. Additionally, we focused upon studies that contained spatially explicit data on fire severity. Additional reviews that discuss fire effects on birds in ponderosa pine and aspen without incorporation of spatially explicit severity data can be found in Saab and Powell (2005), Bock and Block (2005), and Saab *et al.* (2005).

We found that the majority of studies that include reproductive success data in relation to spatially explicit fire severity data have focused upon woodpecker species. Open cup nesters typically have lower nest success compared to cavity nesters (Martin and Li 1992), but it is unknown whether this pattern is true in burned forests. Saab *et al.* (2005) reviewed bird responses to fire in the northern Rocky Mountains, and the preponderance of studies that examine bird reproduction in burned habitats focused upon cavity nesters (woodpeckers, flickers, and western bluebirds

[*Sialia mexicana*]). The studies cited by Saab *et al.* (2005) did not incorporate spatially explicit fire severity data nor did Saab *et al.* (2005) find studies that addressed reproduction of open cup nesters in burned ponderosa pine and aspen forests. Their review is similar to ours in that we, too, did not find studies on reproductive responses of open cup nesters to fire in ponderosa pine and aspen forests. We suggest that such studies should be conducted because species-specific or guild-specific responses to fire severity may differ depending on the ecology of different bird species relative to requirements for food, nesting habitat, and cover.

Few studies have examined space use issues and survivorship in the context of spatially explicit fire severity data. Covert-Bratland *et al.* (2006, 2007) examined hairy woodpecker use of recently burned habitats in the context of fire severity during the non-breeding season and in order to do so, used uniquely marked birds fitted with transmitters. The ability to follow and identify individuals is necessary to obtain data on a species' home range, survivorship, dispersal, and habitat use patterns. Such data are critical for management and conservation of bird species, and are currently lacking in studies of fire effects on birds.

Studies examining the effects of spatially explicit fire severity during the non-breeding season are limited to Covert-Bratland *et al.* (2006, 2007). Although some studies describe winter community composition of birds in burned ponderosa pine forests (e.g., Blake 1982), these studies do not examine communities in the context of fire severity patterns. During the winter, bird populations may be negatively affected by abiotic factors (e.g., weather; Lahti *et al.* 1998), food availability (Lahti *et al.* 1998), and the potential availability of roost sites (Covert-Bratland *et al.* 2007). Food availability and roost sites (for both cavity and open nesters)

are likely to be dynamic in post-fire environments. Therefore, we suggest that additional studies be conducted that address winter requirements of avian species to better understand factors that affect roost site selection and survival.

A variety of species use cavities as a resource, and multiple studies (Martin *et al.* 2004, Gentry and Vierling 2008) suggest that the interactions between cavity excavators and cavity users are important for wildlife management. Nest webs describe the relationship between tree resources, primary cavity excavators (e.g., woodpeckers), and secondary cavity users (i.e., those that use cavities for nesting and roosting; Martin *et al.* 2004). Only one study to date examines nest webs within burned habitats. Such studies may provide information on how selection by primary cavity excavators might affect the overall animal community. Gentry and Vierling (2008) studied nest webs in old (>20 yr post-fire) burned ponderosa pine forests in the Black Hills, and found that a greater diversity of species use northern flicker cavities than cavities excavated by other cavity excavators. Their study is the first to address nest web interactions in the non-breeding season in a stand-replacing burn environment. We suggest that additional research be conducted on nest webs in the breeding and non-breeding season in burned environments to better determine the relative importance of different excavating species to the overall cavity-using community.

The majority of studies conducted thus far have addressed the immediate effects of fire. For instance, all of the bird studies that explicitly incorporated fire severity in their analyses were initiated within the first five years of the burn, and the majority of these studies were fewer than five years in duration. Smucker *et al.* (2005) noted that studies that are short in duration (i.e., 1 yr to 2 yr post-fire) may not be able to detect meaningful trends.

To our knowledge, few studies extend past five years in duration. Saab *et al.* (2007) studied woodpecker responses in burned forests in Idaho for >10 years after the fires, and this represents one of the only examples of a continuously monitored population following fire for that duration. Saab *et al.* (2005) suggested that long term studies of at least 10 years are needed to better understand effects of fire on habitats and bird communities.

Nest-site selection studies have focused upon woodpeckers with different foraging habits (i.e., aerial insectivores and excavators), but we know little about the effects of fire severity on nest-site selection of species that use cavities but do not excavate them (i.e., secondary cavity users). Additionally, no studies, to our knowledge, incorporate spatially explicit fire severity effects in examinations of nest-site selection of open cup nesters in burned ponderosa pine and aspen forests. The lack of studies incorporating spatially explicit fire severity patterns relative to species-specific demography and habitat selection is a major gap in our understanding of fire severity effects on avian communities within ponderosa pine and aspen forests.

Within the studies that we reviewed, researchers used multiple remote sensing classifications to determine fire severity. These included maps generated by Burned Area Emergency Rehabilitation (BAER) teams (Smucker *et al.* 2005), unsupervised classifications of remotely sensed data (e.g., Vierling *et al.* 2008), and differenced Normalized Burn Ratios (e.g., Kotliar *et al.* 2007). Although the purpose of this paper is not to compare these methods, we suggest that future studies assess the outputs of these methods relative to each other. Kotliar *et al.* (2003) compared BAER maps to maps generated using Normalized Burn Ratio (NBR) methods and found that BAER maps tended to overestimate severe burns and underestimate moderate severity burns. We suggest that the

Kotliar *et al.* (2003) approach should be expanded to include more recent approaches to mapping fire severity (i.e., char fraction; Hudak *et al.* 2007, Smith *et al.* 2007) and that future comparisons of fire severity classifications should use metrics that are spatially appropriate for avian species.

Remote sensing provides a powerful tool to evaluate ecological change and make predictions about future habitat conditions. In this review, we highlighted some of the capabilities of remote sensing, yet there are many challenges associated with the broad-scale application of these techniques and resultant comparative assessments. In a review of fire-related remote sensing applications, Lentile *et al.* (2006) recommended that researchers clarify what exactly is being measured versus inferred when these measurements are taken, and avoid categorical or qualitatively based assessments of burn severity. In a comprehensive assessment of nine wildland fires, Hudak *et al.* (2007) concluded that remote sensing data are more strongly correlated with canopy-based metrics than ground-based measures, and that time since fire may strongly impact these relationships. Researchers should also keep in mind that single images provide a snapshot in time, while differencing techniques (e.g., differenced Normalized Burn Ratio) allow for detection of ecological change. With increased reliance on remote sensing, ground-based validation becomes more critical. Researchers must adapt where and how they collect their field data (e.g., plot size, stratification) to the spatial resolution of the sensor and the wide range of conditions represented in the imagery. Researchers need to validate the widely applied differenced Normalized Burn Ratio (dNBR) across the range of environments to ensure that the adopted range of dNBR values is valid for those environments (Key and Benson 2006). As an alternative, Lentile *et al.* (2006) suggest using a process that includes local calibration.

Finally, ecologists have long recognized that large, stand-replacing wildland fires potentially result in enormous variation in soil, plant, and animal responses (Turner *et al.* 1994, Turner *et al.* 1997, Peterson 1998, Lentile *et al.* 2007). Many of these large fires occurred in dry ponderosa and mixed-conifer forests of the west, yet Schnoenagel *et al.* (2004) aptly point out the variation in forest types and fire regimes that occur across the west. The fewer than 10 avian studies cited within this review

represent the current state of knowledge, at the time of writing, relating bird responses to fire severity in ponderosa pine and aspen ecosystems. Given the high variability in structure and fire history in ponderosa pine and aspen ecosystems, multiple studies that are widely distributed within the range of ponderosa pine and aspen are needed to better understand how geographic differences in severity drive variations in avian responses.

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LITERATURE CITED

- Agee, J.K. 1998. The landscape ecology of western forest fire regimes. *Northwest Science* 72: 24-34.
- Agee, J.K. 2005. The complex nature of mixed severity fire regimes. Pages 1-10 in: Proceedings of symposium on mixed severity fire regimes: ecology and management. Association of Fire Ecology, 17-19 November 2004, Spokane, Washington, USA.
- Allen, C.D., M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M. Hoffman, and J.T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine: a broad perspective. *Ecological Applications* 12: 1418-1433.
- Anderson, J.E., and W.H. Romme. 1991. Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. *International Journal of Wildland Fire* 1: 119-124.
- Baker, W.L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research* 31: 1205-1226.
- Bartos, D.L. 2001. Landscape dynamics of aspen and conifer forests. Pages 5-14 in: W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, compilers. Proceedings of the 2000 sustaining aspen in western landscapes symposium. USDA Forest Service Proceedings RMRS-P-18.
- Bartos, D.L., and W.F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. *Journal of Range Management* 34: 315-318.
- Bartos, D.L., J.K. Brown, and G.D. Booth. 1994. Twelve years biomass response in aspen communities following fire. *Journal of Range Management* 47: 79-83.
- Blake, J.G. 1982. Influence of fire and logging on nonbreeding bird communities of ponderosa pine forests in Arizona. *Journal of Wildlife Management* 46: 404-415.
- Bock, C.E., and W.M. Block. 2005. Fire and birds in the southwestern United States. *Studies in Avian Biology* 30: 14-32.

- Bonnet, V.H., A.W. Schoettle, and W.D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. *Canadian Journal of Forest Research* 35: 37-47.
- Brown, J.K., and J.K. Smith, editors. 2000. Wildland fire in ecosystems: effects of fire on flora. USDA Forest Service General Technical Report RMRS-GTR-42-Volume 2.
- Brown, P.M., M.R. Kaufmann, and W.D. Shepperd. 1999. Longterm, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecology* 14: 513-532.
- Brown, P.M., and B. Cook. 2006. Early settlement forest structure in Black Hills ponderosa pine forests. *Forest Ecology and Management* 223: 284-290.
- Brown, S.R., and D.L. Bartos. 2004. Burn severity effects on quaking aspen regeneration. In: Proceedings of the 2004 managing aspen in western landscapes symposium. Utah State University Forestry Extension, 21-23 September 2004, Cedar City, Utah, USA. <http://extension.usu.edu/forestry/UtahForests/Aspen_ShaunaRaeBrown.htm>. Accessed 8 June 2008.
- Campbell, R.B., and D.L. Bartos. 2001. Aspen ecosystems: objectives for sustaining biodiversity. Pages 299-301 in: W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, compilers. Proceedings of the 2000 sustaining aspen in western landscapes symposium. USDA Forest Service Proceedings RMRS-P-18.
- Cocke, A.E., P.Z. Fulé, and J.E. Crouse. 2005. Comparison of burn severity assessments using differenced Normalized Burn Ratio (dNBR) and ground data. *International Journal of Wildland Fire* 14: 189-198.
- Covert-Bratland, K.A., W.M. Block, and T.C. Theimer. 2006. Hairy woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. *Journal of Wildlife Management* 70: 1379-1392.
- Covert-Bratland, K.A., T.C. Theimer, and W.M. Block. 2007. Hairy woodpecker winter roost characteristics in burned ponderosa pine forest. *Wilson Journal of Ornithology* 119: 43-52.
- Covington, W.W., and M.M. Moore. 1994. South-western ponderosa pine forest structure: changes since Euro-American settlement. *Journal of Forestry* 92: 39-47.
- Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *Journal of Forestry* 95: 23-29.
- DeBano, L.F., D.G. Neary, and P.F. Ffolliott. 1998. Fire's effects on ecosystems. John Wiley and Sons, New York, New York, USA.
- Fisher, J.T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35: 51-81.
- Fulé, P.Z., W.W. Covington, H.B. Smith, J.D. Springer, T.A. Heinlein, K.D. Huisinga, and M.M. Moore. 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *Forest Ecology and Management* 170: 19-41.
- Fulé, P.Z., T.A. Heinlein, W.W. Covington, and M.M. Moore. 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *International Journal of Wildland Fire* 12: 129-145.
- Gentry, D.J., and K.T. Vierling. 2007. Old burns as source habitats for Lewis's woodpeckers in the Black Hills of South Dakota. *Condor* 109: 122-131.

- Gentry, D.J., and K.T. Vierling. 2008. Reuse of cavities during the breeding and nonbreeding season in old burns in the Black Hills, South Dakota. *American Midland Naturalist* 160: 413-429.
- Graham, R.T., editor. 2003. Hayman fire case study. USDA Forest Service General Technical Report GTR-RMRS-114.
- Hudak, A.T., P. Morgan, M.J. Bobbitt, A.M.S. Smith, S.A. Lewis, L.B. Lentile, P.R. Robichaud, J.T. Clark, and R.A. McKinley. 2007. The relationship of multispectral satellite imagery to immediate fire effects. *Fire Ecology* 3(1): 64-90.
- Ice, G.G., D.G. Neary, and P.W. Adams. 2004. Effects of wildfire on soils and watershed processes. *Journal of Forestry* 102: 16-20.
- Jain T., D. Pilliod, and R. Graham. 2004. Tongue-tied. *Wildfire* 4: 22-26.
- Kaufmann, M.R., C.M. Regan, and P.M. Brown. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Canadian Journal of Forest Research* 30: 698-711.
- Kay, C.E. 1997. The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: implications for ecological integrity. *Canadian Field-Naturalist* 111: 607-616.
- Keane, R.E., S.F. Arno, and J.K. Brown. 1990. Simulating cumulative fire effects in ponderosa pine/Douglas-fir forests. *Ecology* 71: 189-203.
- Key C.H., and N.C. Benson. 2006. Landscape assessment: ground measure of severity, the Composite Burn Index; and remote sensing of severity, the Normalized Burn Ratio. Pages 1-15 in: D.C. Lutes, R.E. Keane, J.F. Caratti, C.H. Key, N.C. Benson, S. Sutherland, and L.J. Gangi, editors. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service General Technical Report, RMRS-GTR-164-CD: LA 1-51.
- Keyser, T.L., F.W. Smith, and W.D. Shepperd. 2005. Trembling aspen response to a mixed-severity wildfire in the Black Hills, South Dakota, USA. *Canadian Journal of Forest Research* 35: 2679-2684.
- Keyser, T.L., F.W. Smith, L.B. Lentile, and W.D. Shepperd. 2006. Modeling postfire mortality of ponderosa pine following a mixed-severity wildfire in the Black Hills: the role of tree morphology and direct fire effects. *Forest Science* 52: 530-539.
- Kotliar, N.B., S. Hejl, R.L. Hutto, V. Saab, C.P. Melcher, and M.E. McFadzen. 2002. Effects of wildfire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. *Studies in Avian Biology* 25: 49-64.
- Kotliar, N.B., S.L. Haire, and C.H. Key. 2003. Lessons from the fires of 2000: post-fire heterogeneity in ponderosa pine forests. Pages 277-279 in: P.N. Omi, and L.A. Joyce, technical editors. Fire, fuel treatments, and ecological restoration: conference proceedings. USDA Forest Service Proceedings RMRS-P-29.
- Kotliar, N.B., P.L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. *Ecological Applications* 17: 491-507.
- Laughlin, D.C., J.D. Bakker, M.T. Stoddard, M.L. Daniels, J.D. Springer, C.N. Gildar, A.M. Green, and W.W. Covington. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* 199: 137-152.
- Lentile, L.B. 2004. Causal factors and consequences of mixed-severity fire in Black Hills ponderosa pine forests. Dissertation, Colorado State University, Fort Collins, USA.

- Lentile L.B., F.W. Smith, and W.D. Shepperd. 2005. Patch structure, fire-scar formation and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. *Canadian Journal of Forest Research* 35: 2875-2885.
- Lentile, L.B., Z.A. Holden, A.M.S. Smith, M.J. Falkowski, A.T. Hudak, P. Morgan, S.A. Lewis, P.E. Gessler, and N.C. Benson. 2006. Remote sensing techniques to assess active fire characteristics and post-fire effects. *International Journal of Wildland Fire* 15: 319-345.
- Lentile, L.B., P. Morgan, A.T. Hudak, M.J. Bobbitt, S.A. Lewis, A.M.S. Smith, and P.R. Robichaud. 2007. Post-fire burn severity and vegetation response following eight large wildfires across the western United States. *Fire Ecology* 3(1): 91-108.
- Lewis, S.A., J.Q. Wu, and P.R. Robichaud. 2006. Assessing burn severity and comparing soil water repellency, Hayman Fire, Colorado. *Hydrological Processes* 20: 1-16.
- Lewis, S.A., P.R. Robichaud, B.E. Frazier, J.Q. Wu, and D.Y.M. Laes. 2008. Using hyperspectral imagery to predict post-wildfire soil water repellency. *Geomorphology* 95: 192-205.
- Lyon, L.J., and P.F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. *Proceedings of the Tall Timbers Fire Ecology Conference* 14: 355-375.
- Martin, K., K.E.H. Aitken, and K.L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106: 5-19.
- Martin, T.E., and P. Li. 1992. Life history traits of open- versus cavity-nesting birds. *Ecology* 73: 579-592.
- Martin, T.E. 1993. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43: 523-532.
- Morgan, P., C. Hardy, T. Swetnam, M.G. Rollins, and L.G. Long. 2001. Mapping fire regimes across time and space: understanding coarse- and fine-scale fire patterns. *International Journal of Wildland Fire* 10: 329-342.
- Morgan, P., G.E. Defosse, and N.F. Rodriguez. 2003. Management implications of fire and climate changes in the western Americas. Pages 413-440 in: T.T. Veblen, W.L. Baker, G. Montenegro, and T.W. Swetnam, editors. *Fire and climatic change in temperate ecosystems of the western Americas*. Ecological Studies 160. Springer-Verlag, New York, New York, USA.
- Mutch, R.W. 1970. Wildland fires and ecosystems—a hypothesis. *Ecology* 51: 1046-1051.
- Peterson, D.L. 1998. Large-scale fire disturbance: from concepts to models. *Northwest Science* 72: 1-3.
- Romme, W.H., L. Floyd-Hanna, D. Hanna, and E. Bartlett. 2001. Aspen's ecological role in the west. Pages 243-259 in: W.D. Shepperd; D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, compilers. *Proceedings of the 2000 sustaining aspen in western landscapes symposium*. USDA Forest Service Proceedings RMRS-P-18.
- Romme, W.H., M.G. Turner, L.L. Wallace, and J.S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. *Ecology* 76: 2097-2106.
- Rumble, M.A., and S.H. Anderson. 1996. Feeding ecology of Merriam's turkeys (*Meleagris gallopavo merriami*) in the Black Hills, South Dakota. *American Midland Naturalist* 136: 157-171.
- Saab, V.A, and K.T. Vierling. 2001. Reproductive success of Lewis's woodpecker in burned pine and cottonwood riparian forests. *Condor* 103: 491-501.
- Saab, V.A., and H.D.W. Powell. 2005. Fire and avian ecology in North America: process influencing pattern. *Studies in Avian Biology* 30: 1-13.

- Saab, V., J. Dudley, and W. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. *Condor* 106: 20-36.
- Saab, V.A., H.D.W. Powell, N.B. Kotliar, and K.R. Newlon. 2005. Variation in fire regimes of the Rocky Mountains: implications for avian communities and fire management. *Studies in Avian Biology* 30: 76-96.
- Saab, V.A., R.E. Russell, and J.G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *Condor* 109: 97-108.
- Schoenagel T.L., T.T. Veblen, and W.H. Romme. 2004. The interaction of fire, fuels and climate across Rocky Mountain forests. *BioScience* 54: 661-676.
- Shearer, R.C., and P.F. Stickney. 1991. Natural revegetation of burned and unburned clearcuts in western larch forests of northwest Montana. Pages 66-74 in: S.C. Nodvin, and T.A. Waldrop, editors. Proceedings of an international symposium on fire and the environment: ecological and cultural perspectives. USDA Forest Service General Technical Report GTR-SE-69.
- Shinneman, D.J., and W.L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conservation Biology* 11: 1276-1288.
- Smith, A.M.S., L.B. Lentile, A.T. Hudak, and P. Morgan. 2007. Evaluation of linear spectral unmixing and dNBR for predicting post-fire recovery in a North American ponderosa pine forest. *International Journal of Remote Sensing* 28: 5159-5166.
- Smith, J.K., editor. 2000. Wildland fire in ecosystems: effects of fire on fauna. USDA Forest Service General Technical Report RMRS-GTR-42-Volume 1.
- Smith, K.G., J.H. Withgott, and P.G. Rodewald. 2000. Red-headed woodpecker (*Melanerpes erythrocephalus*). Account 518 in: A. Poole, and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Smucker, K.M., R.L. Hutto, and B.M. Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15: 1535-1549.
- Stephens, S.L., and W.L. Ruth. 2005. Federal forest-fire policy in the United States. *Ecological Applications* 15: 532-542.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M.C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79-92.
- Turner, M.G., W.L. Baker, C.J. Peterson, and R.K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1: 511-523.
- Turner, M.G., W.W. Hargrove, R.H. Gardner, and W.H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* 5: 731-742.
- Turner, M.G., W.H. Romme, and R.H. Gardner. 1999. Pre-fire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9: 21-36.
- Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411-433.
- Vierling, K.T., and L.B. Lentile. 2006. Red-headed woodpecker nest-site selection and reproduction in mixed ponderosa pine and aspen woodland following fire. *Condor* 108: 957-962.

- Vierling, K.T., L.B. Lentile, and N. Nielsen-Pincus. 2008. Pre-burn forest characteristics and woodpecker use in burned coniferous forests. *Journal of Wildlife Management* 72: 422-427.
- Wagle, R.F., and J.H. Kitchen. 1972. Influence of fire on soil nutrients in a ponderosa pine type. *Ecology* 53: 118-125.
- Wells C.G., R.E. Campbell, L.F. DeBano, C.E. Lewis, R.L. Fredriksen, E.C. Franklin, R.C. Froelich, and P.H. Dunn. 1979. Effects of fire on soil, a state-of-knowledge review. USDA Forest Service General Technical Report WO-7.
- Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. *Science* 313: 940-943.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66: 1211-1214.