

Quantifying the multi-scale response of avifauna to prescribed fire experiments in the southwest United States

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Abstract. Landscape-scale disturbance events, including ecological restoration and fuel reduction activities, can modify habitat and affect relationships between species and their environment. To reduce the risk of uncharacteristic stand-replacing fires in the southwestern United States, land managers are implementing restoration and fuels treatments (e.g., mechanical thinning, prescribed fire) in progressively larger stands of dry, lower elevation ponderosa pine (*Pinus ponderosa*) forest. We used a Before–After/Control–Impact experimental design to quantify the multi-scale response of avifauna to large (~250–400 ha) prescribed fire treatments on four sites in Arizona and New Mexico dominated by ponderosa pine. Using distance sampling and an information-theoretic approach, we estimated changes in density for 14 bird species detected before (May–June 2002–2003) and after (May–June 2004–2005) prescribed fire treatments. We observed few site-level differences in pre- and posttreatment density, and no species responded strongly to treatment on all four sites. Point-level spatial models of individual species response to treatment, habitat variables, and fire severity revealed ecological relationships that were more easily interpreted. At this scale, pretreatment forest structure and patch characteristics were important predictors of posttreatment differences in bird species density. Five species (Pygmy Nuthatch [*Sitta pygmaea*], Western Bluebird [*Sialia mexicana*], Steller's Jay [*Cyanocitta stelleri*], American Robin [*Turdus migratorius*], and Hairy Woodpecker [*Picoides villosus*]) exhibited a strong treatment response, and two of these species (American Robin and Hairy Woodpecker) could be associated with meaningful fire severity response functions. The avifaunal response patterns that we observed were not always consistent with those reported by more common studies of wildland fire events. Our results suggest that, in the short term, the distribution and abundance of common members of the breeding bird community in Southwestern ponderosa pine forests appear to be tolerant of low- to moderate-intensity prescribed fire treatments at multiple spatial scales and across multiple geographic locations.

Key words: BACI design; birds; density; distance sampling; fire severity; forest structure; fuel reduction treatments; model selection; ponderosa pine; prescribed fire; restoration; scale.

INTRODUCTION

Human-caused disturbance events, such as broadscale land conversion, road building, and fire, can have significant impacts on ecological communities (Dale et al. 2005). Similarly, large-scale ecological restoration activities designed to promote ecosystem health and protect human communities (e.g., fuels reduction in fire-adapted forests; Dombek et al. 2004) can modify habitat and affect relationships between species and their environment. As the size and pace of restoration and fuels reduction efforts increase, stakeholders require information summarizing the impacts of treatments on meaningful ecosystem attributes (Sisk et al. 2006).

Forest restoration attempts to establish self-sustaining system processes by manipulating succession and mimicking recovery from natural disturbance (Angermeier and Karr 1994, Covington 2003). In recent decades, actions to restore the structure and function of western coniferous forests in North America have accelerated, but debate continues about how best to treat forests and minimize ecological degradation (Allen et al. 2002). For example, restoration projects in the southwestern United States are removing forest biomass using mechanical thinning and fire treatments to create forest structure conditions presumed to exist prior to Euro-American settlement of the region (Covington et al. 1997). However, restoration ecologists remain unsure about how to return forests to a more natural condition and, at the same time, maintain biodiversity across large areas where fire behavior, fuel quantities, and forest structure have been changed by humans (Noss et al. 2006).

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In fire-adapted coniferous forests of the United States, prescribed fire treatments have been offered as a primary tool to improve ecosystem health and function (Mutch 1995, Kauffman 2004), mitigate wildland fire size and severity (Schoennagel et al. 2004, Finney et al. 2005), and reconcile the goals of fuel treatments and ecological restoration (Allen et al. 2002; see Plate 1). This primacy notwithstanding, there remain significant uncertainties about the immediate and long-term consequences of reintroducing fire on the conservation of animal populations and on the habitats that support biological communities (Tiedemann et al. 2000). Across North America, declines in historically common vertebrate taxa, such as forest birds, are being observed with increasing frequency, although the factors influencing these trends are less clear (DeSante and George 1994, Donovan and Flather 2002). In southwestern forests, declines in avifauna may be exacerbated by climate change (e.g., Martin 2007) and an ensuing increase in fire frequency and severity that could be expected under future climate conditions (McKenzie et al. 2004). Because of these uncertainties, it is important to provide land managers with information needed to understand and minimize any adverse effects of prescribed fire treatments on wildlife.

Birds are often the focal taxon in studies of wildlife response to disturbance, including natural- and human-caused fire (see reviews by Kotliar et al. 2002, Saab and Powell 2005). This literature is characterized by conflicting conclusions (Hejl 1994, van Mantgem et al. 2001), with differences in geographic context, dominant vegetation, fire intensity, severity, and season (Rotenberry et al. 1995, Kotliar et al. 2002, Bock and Block 2005a), as well as methodological differences in study design (see Finch et al. 1997) contributing to the equivocation. To remedy this situation, researchers and managers have called for increased rigor in studies of disturbance effects on avian populations (Van Horne 2005) and have emphasized a need for replicated experiments that examine avifaunal response to forest treatments, including prescribed fire (Finch et al. 1997, Kotliar et al. 2002, Bock and Block 2005a).

Typically, studies of prescribed fire are conducted on treatment units too small (e.g., <100 ha) to measure change in the distribution and abundance of highly vagile taxa, including birds (Block et al. 2001, Dickson et al. 2004). As a result, there is limited empirical evidence to evaluate whether avian species are reliable indicators of ecosystem response to forest management activities that use introduced fire across larger areas. Furthermore, it is unclear how prefire forest structural attributes, bird autecology, and fire behavior interact to cause changes in postfire bird assemblages. For example, different species may respond differently to varying levels of fire severity because of distinct habitat requirements and because inherent variability in fire severity can result in a mosaic of treatment effects on forest structure.



PLATE 1. Prescribed fire on the Lakeside Ranger District, Apache-Sitgreaves National Forest, in the White Mountains of eastern Arizona, USA. Photo credit: USDA Forest Service.

In the American Southwest, land managers are interested in reintroducing fire to progressively larger stands of dry, lower-elevation ponderosa pine (*Pinus ponderosa*) forest (see Allen et al. 2002). This regional context provided us with the unique opportunity to quantify the response of avifauna to multiple large-scale prescribed fire treatments implemented in a common fashion. Specifically, we used a designed experiment to: (1) quantify ponderosa pine-dominated forest structure and physiographic habitat attributes at multiple spatial scales prior to treatment; (2) identify treatment-induced changes in the density of individual avian species while accounting for factors that affected detection probability; and (3) use spatial models to quantify the response of individual species density as a function of prefire habitat attributes and levels of fire severity selected a priori. Because the use of prescribed fire has the potential to transform avifaunal communities (e.g., increase or decrease species density) and modify their habitats at multiple spatial scales (Finch et al. 1997, Brawn et al. 2001), we chose to focus on individual species whose density could be reliably estimated at spatial scales relevant to forest management practices. Moreover, we expected this approach to reveal a suite of “fire response” species that could be identified from among the most frequently detected species, and a subset of species that could be predictably associated with quantitatively derived levels of fire severity.

METHODS

Study area

We established four experimental study sites on four national forests in northern Arizona and west-central New Mexico, USA (Fig. 1). Overstory vegetation on each site was dominated (relative contribution to canopy cover $\geq 70\%$) by ponderosa pine (Dickson 2006). We attempted to select sites with trees from multiple age

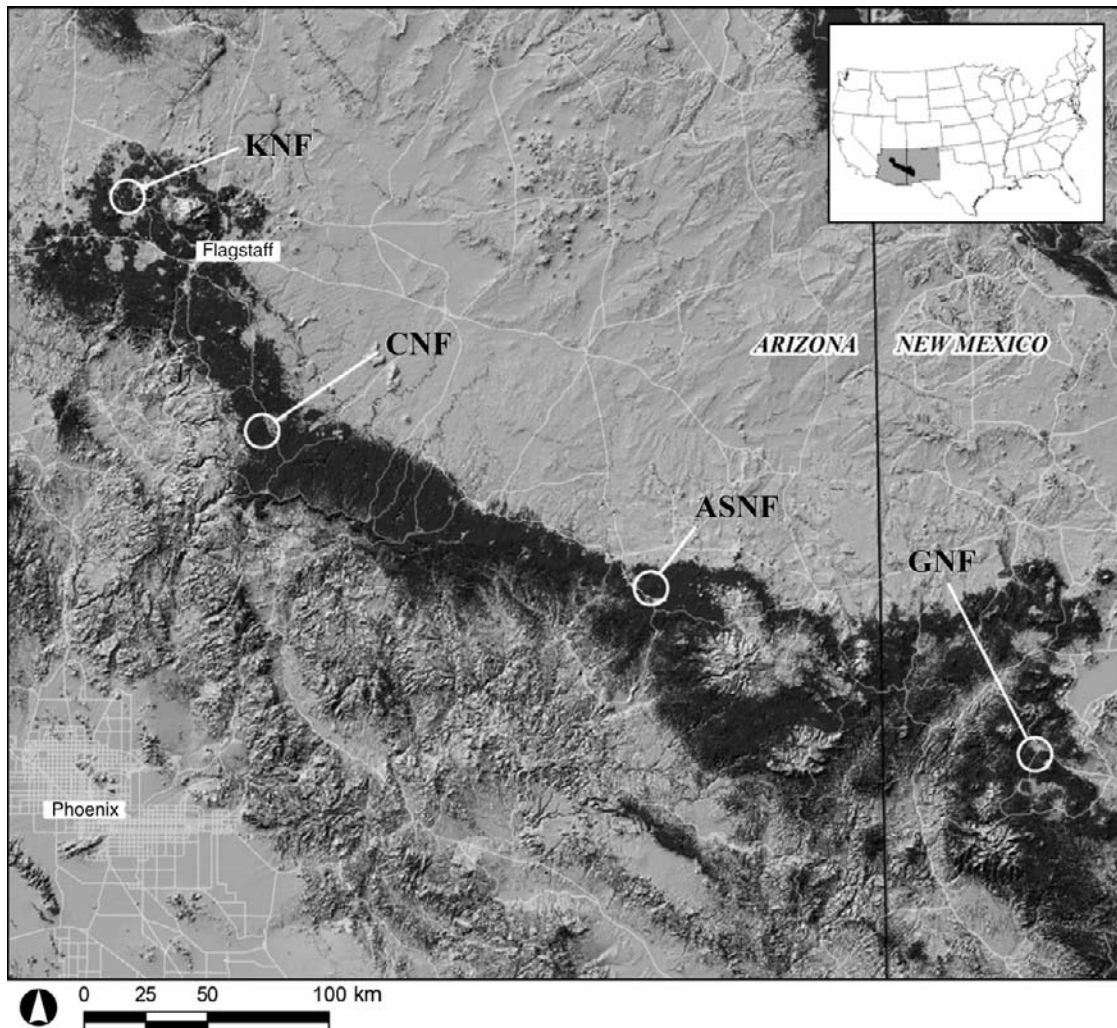


FIG. 1. Locations of the four study sites (white-outlined open circles) in Arizona and New Mexico, USA, used to evaluate avifaunal response to prescribed fire treatments in ponderosa pine forests in the Kaibab National Forest (KNF), Coconino National Forest (CNF), Apache-Sitgreaves National Forest (ASNF), and Gila National Forest (GNF), 2002–2005. Dark shading indicates areas of ponderosa pine-dominated forest along the Mogollon Rim.

classes, and that had escaped large-scale logging or fuels treatment in recent decades. Sites were located on the Kaibab National Forest (KNF), the Coconino National Forest (CNF), and the Apache-Sitgreaves National Forest (ASNF) in Arizona and the Gila National Forest (GNF) in New Mexico. The KNF and GNF sites were established in May 2002 and the CNF and ASNF sites in May 2003.

Between September 2003 and May 2004, prescribed fire treatments were implemented by U.S. Forest Service District personnel at each of the four study sites. Two treatments were completed in the fall of 2003 (ASNF, CNF) and two in the spring of 2004 (GNF, KNF). All prescriptions were characterized as broadcast burns with expected fire behaviors of low to moderate intensity (see also Dickson 2006).

Data collection

Sampling design.—We used a multisite Before–After/Control–Impact (BACI; Green 1979) experimental design to assess the response variables (Appendix A defines each of the variables and scales of association that we investigated). Each study site represented a single replicate consisting of prescribed fire “treatment” and “control” units that contained between 50 and 90 permanent sampling points at which all variables were measured (10–40 points per unit; 134 treatment and 144 control points = 278 total points). Each 247–405 ha treatment unit was paired with one (CNF, GNF) or two (ASNF, KNF) nearby (1–5 km) control units of similar extent and with similar vegetation cover. We used a geographic information system (ArcGIS 8.1; ESRI, Redlands, California, USA) to systematically randomly place prospective sampling locations ≥ 250 m apart, and

a global positioning system to locate and permanently mark sampling points on the ground. Dickson (2006) provides a detailed description of study sites and sampling design.

Local-scale habitat attributes.—We summarized nine local-scale forest structure habitat attributes using ground-based sampling centered on each of the 278 points. To characterize these attributes prior to treatments, we placed a 50-m transect line in each of the four cardinal directions and measured the diameter at breast height (dbh) or root-crown diameter (*Juniperus* species) of all live tree species encountered ≤ 5 m of either side of the transect line (Saab et al. 2006). At each point, we estimated tree species richness, the proportion (i.e., dominance) of ponderosa pine stems, and total tree density (stems/ha) and basal area (m^2/ha) by combining data for larger ($\text{dbh} \geq 23$ cm) and smaller trees measured ≤ 5 m and ≤ 2 m from each transect line, respectively. For all large live trees, we also estimated mean and variance of tree height. We used a digital camera and imaging software to derive overstory canopy closure values from fisheye photographs (Frazer et al. 1999). We computed the density of large ($\text{dbh} \geq 23$ cm) snags and a decay index for snags ≤ 10 m from each transect line using methods described by Dickson (2006).

Patch-scale habitat attributes.—To quantify forest habitat characteristics at the patch scale, we used the GIS to derive elevation and slope from a mosaic of USGS digital elevation models and we computed mean values for these variables using a neighborhood function and a circular moving window with a 100 m radius. We derived three models of pretreatment forest structure using remotely sensed image analyses and the GIS, including canopy cover (0–100%), basal area (m^2/ha), and tree density (individual trees/ha) (Sisk et al. 2006, Xu et al. 2006). To identify discrete patch types, we synthesized the three structure attributes using a fuzzy classification algorithm in the BoundarySeer software package (TerraSeer, Crystal Lake, Illinois, USA). We grouped the forest structure data into three classes, or “types,” of structural composition: open, less dense, and more dense (Appendix B). We used neighborhood functions in the GIS to compute (1) which patch type occurred most frequently (variable = “PatchType”) and (2) patch heterogeneity or “richness” (“PatchRich”) within a 100 m radius of each survey point. We treated the physiographic variables as continuous, and the PatchType and PatchRich variables as ordinal in the habitat models that we will describe (see also Dickson 2006).

Avifaunal sampling.—We measured avifaunal community composition and species response to prescribed fire using a sampling design that provided estimates of density by distance-based methods (Buckland et al. 2001, Dickson 2006). During the breeding season (May–June) of the pre- (2002–2003) and posttreatment (2004–2005) years, a team of experienced observers counted birds at each site using point-transect distance sampling. At each point we recorded the distance of all species

detected by sight or sound in five predefined distance bins (10, 25, 50, 75, 100 m) within a 5-minute period. Observers used laser range finders to improve the accuracy of their distance estimates. Individual observers randomly visited 8–10 points per unit per day and sampled each point 3–4 times each season.

Data analyses

Local-scale habitat variable reduction.—We synthesized habitat data using a factor analysis and extraction by principal components analysis (PCA) and retained only those habitat factors with eigenvalues > 1.0 (Manly 2005, Dickson 2006). To simplify interpretation, we used varimax rotation with Kaiser normalization to compute the sums of squared loadings for each factor (Manly 2005). Subsequently, we used the rotated factor loadings to interpret the principal components based on the sign and the magnitude of the loadings among those variables with an absolute value ≥ 0.50 (Manly 2005). For these analyses, we pooled data from all ($n = 278$) points and retained factor scores as independent, local-scale habitat variables in our point-level response models. All analyses were performed using SPSS V14.0 (SPSS, Chicago, Illinois, USA).

Prescribed fire severity.—To quantify the influence of treatments on forest structure and birds, we derived a fire severity variable using five tree damage variables measured at each point: maximum bole char severity, average maximum bole scorch height, average percentage of the bole circumference charred, average proportional crown scorch, and average proportional crown consumption, all measured within six months of treatment (see Breece et al. 2008). For parsimony, we defined three clusters, or “levels” of fire severity at each point: low, moderate, and high, using a likelihood-based two-step cluster analysis (Chiu et al. 2001) implemented in SPSS, capable of accommodating mixed variable types (for details, see Dickson 2006).

Estimating avian species density changes.—We used program DISTANCE V5.0 (Thomas et al. 2005) and multi-model inference to estimate avian species density ($\hat{D}$) and to control for differences in detection probability ($\hat{p}$) among treatments over time (Buckland et al. 2001, Norvell et al. 2003). Because we were most interested in a set of species that could be detected frequently, we focused our analyses on those species with > 500 total detections across all years. We considered this group of species to be our “inference set.” Within DISTANCE, we modeled detection probabilities for individual species as a function of multiple-factor covariates that may have influenced detectability of a given species, including site ($n = 4$ factor levels), year ($n = 3$ or 4), and observer rank ($n = 3$). Observer rank was a categorical rating (1, 2, or 3) of observer quality (1 = high) based on a comparison of detection histograms and field performance evaluations. Although we initially considered additional habitat and treatment feature covariates (e.g., tree density, percent canopy cover, ratio

of burned:unburned) that may affect detection probability, preliminary models that included these covariates had little or no support. We modeled a global detection function (Buckland et al. 2001) and considered all possible combinations of the three factor covariates in our candidate model set, in addition to a null model. To address model selection uncertainty, we used model-averaging methods (Burnham and Anderson 2002).

We used DISTANCE to estimate density at two spatiotemporal levels: “stratum” and “point.” Strata were defined by combining bird detections among points that were on the unburned treatment (E1) or control (C1) units in pretreatment years (2002, 2003) and the burned treatment (E2) or control (C2) units in post-treatment years (2004, 2005) at each site. Density at the stratum level was estimated by pooling together detections for the pretreatment period (years 2002, 2003) on the unburned treatment (stratum-level estimate = $\hat{D}_s^{E1}$) and control ($\hat{D}_s^{C1}$) units and separately for the posttreatment period (2004, 2005) on the burned treatment ($\hat{D}_s^{E2}$) and control ($\hat{D}_s^{C2}$) units. For inference at the site level, s , we then computed the difference in estimated pretreatment density as

$$\hat{D}_s^{\text{PRE}} = (\hat{D}_s^{E1} - \hat{D}_s^{C1}) \quad (1)$$

and the difference in estimated posttreatment density as

$$\hat{D}_s^{\text{POST}} = (\hat{D}_s^{E2} - \hat{D}_s^{C2}). \quad (2)$$

Finally, for each of the four study sites, we computed the among-stratum BACI difference, or effect size as

$$\hat{\Delta}_s = (\hat{D}_s^{\text{POST}} - \hat{D}_s^{\text{PRE}}). \quad (3)$$

At the stratum level, and for each species with a large sample size (typically, $n > 1000$ detections), estimates for density difference ($\hat{\Delta}_s$) and its variance ($\text{Var}(\hat{\Delta}_s)$) were generated using 1000 bootstrap samples (within strata). For all other species ($500 < n < 1000$) we used a modified delta method (Buckland et al. 2001) to estimate $\text{Var}(\hat{\Delta}_s)$ (see Appendix C for details). Although we were interested in the magnitude of $\hat{\Delta}_s$, by convention, we used a Z statistic to test the null hypothesis $D_s^{\text{POST}} = D_s^{\text{PRE}}$ at $\alpha = 0.05$ (Buckland et al. 2001).

We generated estimates for density at the point level by pooling all detections for a given species over pre- or posttreatment years. Because point-level sample sizes were always small, we modeled the variance-covariance structure of the point-level density estimates to identify and account for any residual correlation and interdependencies among samples. For each point, i , where $i = 1, 2, \dots, n$, and n is the 278 points, we computed the difference in pre- and posttreatment density as

$$\hat{\Delta}_i^* = (\hat{D}_i^{E2} - \hat{D}_i^{E1})$$

or

$$(\hat{D}_i^{C2} - \hat{D}_i^{C1}). \quad (4)$$

These point-level difference estimates were used as the response variable in the individual species habitat and fire response models that we will describe.

Avian species habitat and fire-response modeling.—To examine point-level response of individual species, we modeled the spatiotemporal relationship between $\hat{\Delta}_i^*$ and the habitat predictor variables using a spatial mixed model (MIXED procedure in SAS V9.1; SAS Institute, Cary, North Carolina, USA). Variables included standardized mean elevation and slope, PatchType, PatchRich, and the local-scale habitat factors. We also included a “treatment” variable to indicate the control (“0”) or treatment unit (“1”), and indexed each site as a random effect. We modeled the mean response of individual species to four ordinal levels of fire severity (none, low, moderate, and high) only when they exhibited a strong response to the treatment variable. We evaluated three possible functional forms of this response: linear, log normal, and second-degree polynomial.

Because point-level density estimates may be spatially dependent, we modeled their covariance structure (i.e., positive spatial correlation among points in a given unit). Importantly, this approach allowed us to account for any among-point interdependencies that existed because of a shared $\hat{p}$ (i.e., one estimated using a global detection function) among points. To estimate covariance parameters and determine the “best” covariance model form (Littell et al. 1996), we fit empirical semivariograms and computed values of AIC_c, Akaike’s Information Criterion corrected for small sample size (Burnham and Anderson 2002).

We used AIC_c values and Akaike weights of evidence to assess model fit and ranked relative variable importance by summing the Akaike weights across all ($n = 256$) possible models in which a given variable occurred (Burnham and Anderson 2002). We interpreted these cumulative Akaike weights (w_+) as relative probabilities of importance, considered values ≥ 0.50 to be strong evidence for a species response to the treatment variable (Barbieri and Berger 2004), and constructed mean fire-response models only for those species with these evidence values. We used AIC_c values to identify the best functional form of the response of each species to levels of fire severity. We used the Tukey-Kramer multiple comparison to test for differences among levels of fire severity ($\alpha = 0.05$).

RESULTS

Preliminary analyses

Local-scale habitat variable reduction.—The results of the point-level habitat PCA indicated that three factors adequately (eigenvalues > 1.00) summarized nine prefire forest structure attributes and explained 66.6% of the total variance (Appendix D). For the three retained habitat factors, loadings suggested that mean tree height, ponderosa pine dominance, large snag decay, large tree richness, and canopy closure were most

TABLE 1. Cumulative Akaike weights (w_+) for assessing the relative importance of habitat variables used to predict the mean point-level response ($\hat{\Delta}_i^*$) of bird density to prescribed fire for 14 inference species on four sites in Arizona and New Mexico, USA.

Species	Scientific name	Total detections	Treatment	Elevation	Slope	Patch-Type	Patch-Rich	FAC_1	FAC_2	FAC_3
Dark-eyed Junco	<i>Junco hyemalis</i>	2713	0.332	0.376	0.298	0.287	0.733	0.437	0.432	0.295
Pygmy Nuthatch	<i>Sitta pygmaea</i>	1839	0.752	0.593	0.394	0.790	0.311	0.371	0.693	0.418
Western Bluebird	<i>Sialia mexicana</i>	1553	0.561	0.613	0.330	0.293	0.261	0.288	0.267	0.563
Grace's Warbler	<i>Dendroica graciae</i>	1468	0.286	0.998	0.446	0.298	0.300	0.583	0.420	0.278
Mountain Chickadee	<i>Poecile gambeli</i>	1285	0.415	0.502	0.322	0.746	0.276	0.989	0.874	0.313
Western Tanager	<i>Piranga ludoviciana</i>	1251	0.314	0.842	0.483	0.510	0.264	0.580	0.348	0.425
Yellow-rumped Warbler	<i>Dendroica coronata</i>	1165	0.283	0.991	0.638	0.307	0.393	0.713	0.503	0.461
White-breasted Nuthatch	<i>Sitta carolinensis</i>	1085	0.342	0.574	0.423	0.324	0.288	0.291	0.770	0.273
Plumbeous Vireo	<i>Vireo plumbeus</i>	1061	0.322	0.638	0.681	0.342	0.316	0.352	0.712	0.387
Steller's Jay	<i>Cyanocitta stelleri</i>	815	0.642	0.673	0.370	0.338	0.413	0.471	0.261	0.616
American Robin	<i>Turdus migratorius</i>	637	0.997	0.287	0.427	0.304	0.299	0.321	0.536	0.561
Chipping Sparrow	<i>Spizella passerina</i>	628	0.379	0.999	0.505	0.814	0.285	0.604	0.872	0.829
Western Wood-Pewee	<i>Contopus sordidulus</i>	602	0.263	0.565	0.363	0.643	0.687	0.280	0.266	0.426
Hairy Woodpecker	<i>Picoides villosus</i>	577	0.866	0.296	0.582	0.707	0.417	0.897	0.262	0.309
Mean			0.482	0.639	0.447	0.479	0.374	0.513	0.515	0.440

Notes: Weights are interpreted as relative probabilities of importance. Variable names are defined in Appendix A: PatchType is the most frequent patch type; PatchRich is patch richness; FAC_1, 2, and 3, respectively, are local-scale habitat factors 1, 2, and 3. Species are arranged based on greatest to fewest numbers of detections.

important, whereas tree density and basal area were moderately important (Appendix D). Large-snag sum and SD tree height were less important descriptors (loadings < 0.50). We considered points with higher values for habitat factor 1 (FAC_1) to be characterized by increased decay levels in the larger snags, higher stem densities, and greater tree species richness. Higher values for habitat factor 2 (FAC_2) were indicative of points dominated by more open stands of older ponderosa pine, and higher values for factor 3 (FAC_3) were characterized by points with high values for canopy closure and basal area.

Summary of avian detections.—Between May and June 2002–2005, we recorded 31 374 individual detections of 82 avian species during 3666 sampling occasions on the four study sites (Dickson 2006). Excluding detections that were >100 m, flyovers, and incidental observations, we considered 21 612 detections among 74 species for analysis. Of these species, 32 (43%) were detected on all four sites and 14 of these species were detected >500 times, comprising ~77% of all detections (Table 1). The mean number of detections among all 74 species was 281.2 (SD = 514.6) and most species were detected on two or three sites.

Avian response to prescribed fire and habitat

Avian species density response to prescribed fire treatments.—We estimated density for the 14 species with >500 total detections and this group of species became the inference set in our statistical models of individual density response to prescribed fire treatments. In general, model selection uncertainty due to the multiple-factor covariates used to model $\hat{p}$ for each of these species was minimal (Dickson 2006). We detected a statistically significant difference ($\hat{\Delta}_s$) in pre- and posttreatment density on ≥ 1 of the four sites for eight

of the species in our inference set (Fig. 2). Two (Western Tanager [*Piranga ludoviciana*] and Hairy Woodpecker [*Picoides villosus*]) of these eight species exhibited a significant positive response on two sites and none responded on more than two sites. Only three (Western Bluebird [*Sialia mexicana*], Steller's Jay [*Cyanocitta stelleri*], and Hairy Woodpecker) of these eight species responded in a consistent direction (positive) across sites ($Z > 0$). Of the six species that did not exhibit a statistically significant difference at the site level, the Plumbeous Vireo (*Vireo plumbeus*) and Western Wood-Pewee (*Contopus sordidulus*) consistently responded in a positive or negative direction, respectively. However, Western Wood-Pewee was the only species to show a statistically significant overall (mean among means) decline following treatment ($Z = -4.919$, $P < 0.001$).

Models of the mean point-level response ($\hat{\Delta}_i^*$) of the 14 species suggested that elevation was the most important variable (mean $w_+ = 0.639$), followed by two of the three local-scale habitat factors (FAC_2 = 0.515, FAC_1 = 0.513) and treatment (0.482; Table 1). Among our inference set of species, weights of evidence suggested that most of these species were more strongly associated with pretreatment habitat variables than with the treatments themselves. The treatment variable had the most weight only for the American Robin (*Turdus migratorius*; 0.997). Regression coefficients suggested a positive or negative point-level response to treatment by 11 and three species, respectively, although the magnitude of these values was usually small (Table 2). Elevation was typically ($n = 6$ species) the variable with the maximum weight. Coefficients for elevation were negative for all but two species (White-breasted Nuthatch [*Sitta carolinensis*] and American Robin). Most species responded positively ($n = 11$) to increasing values

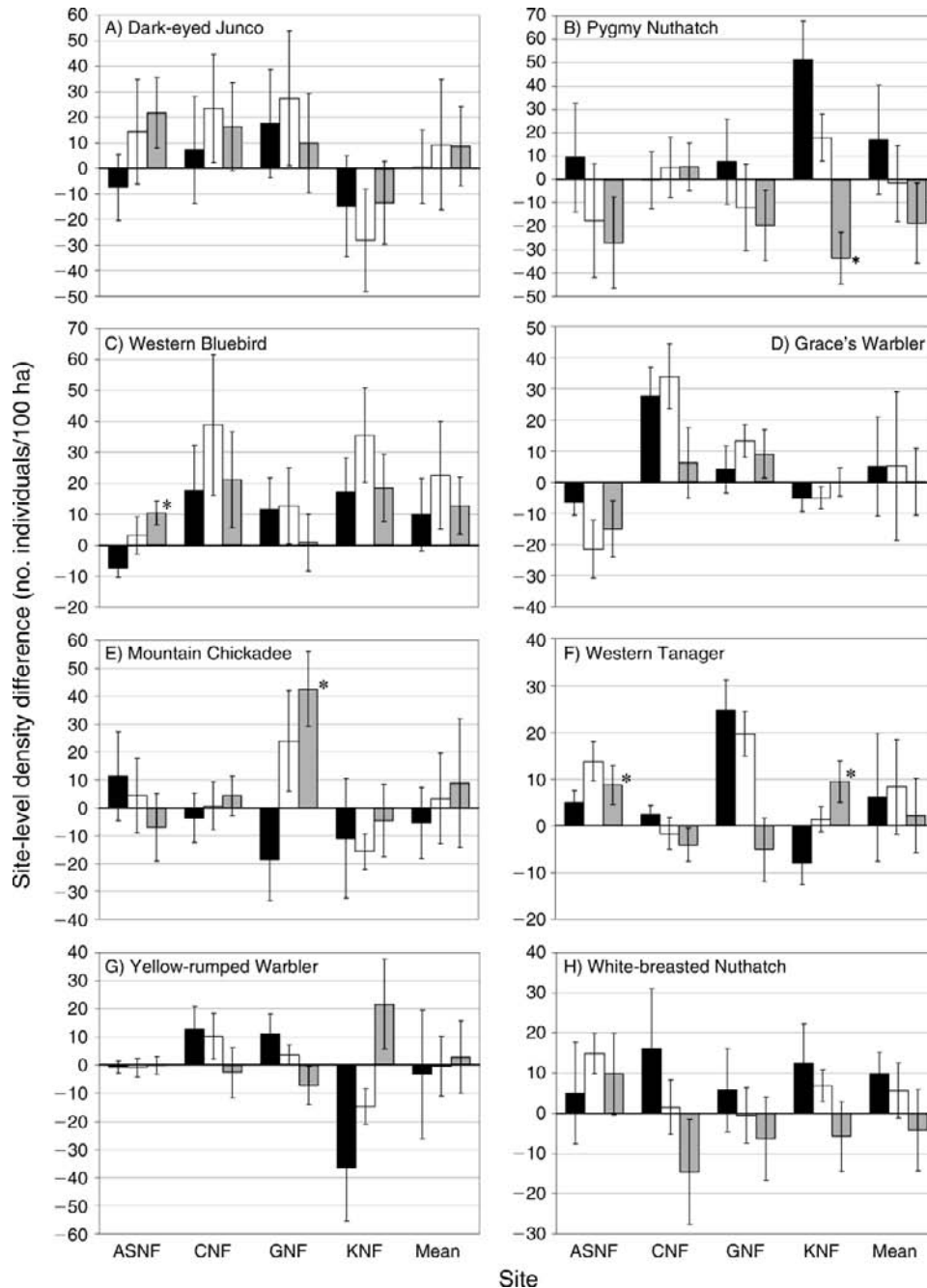


FIG. 2. Differences in the site-level density (individuals/100 ha) estimates for the 14 bird species in the inference set, on four study sites in Arizona and New Mexico. Difference estimates (mean $\pm$ SE) for each species were derived for pretreatment years on the unburned treatment and control units (black bars) and separately for posttreatment years on the burned treatment and control units (white bars). Gray bars represent the difference in these site-level differences (Δ_s). Negative difference estimates indicate that fewer individuals were detected on prescribed fire treatment units compared to control units. Negative or positive estimates for the difference in the differences indicate a negative or positive overall response to the treatments, respectively. An asterisk next to the difference in differences indicates a statistically significant ($P \leq 0.05$) Z statistic. Species are arranged (A–N) based on greatest to fewest numbers of detections. Site abbreviations are spelled out in Fig. 1.

of the FAC_1 habitat factor and negatively ($n = 10$) to increasing values of FAC_2.

Response of avian species density to prescribed fire severity.—We examined the response of five species (for

the treatment variable, $w_+ \geq 0.50$) to levels of fire severity: Pygmy Nuthatch (*Sitta pygmaea*), Western Bluebird, Steller's Jay, American Robin, and Hairy Woodpecker (Fig. 3). For Pygmy Nuthatch ($w_+ = 0.75$), Western

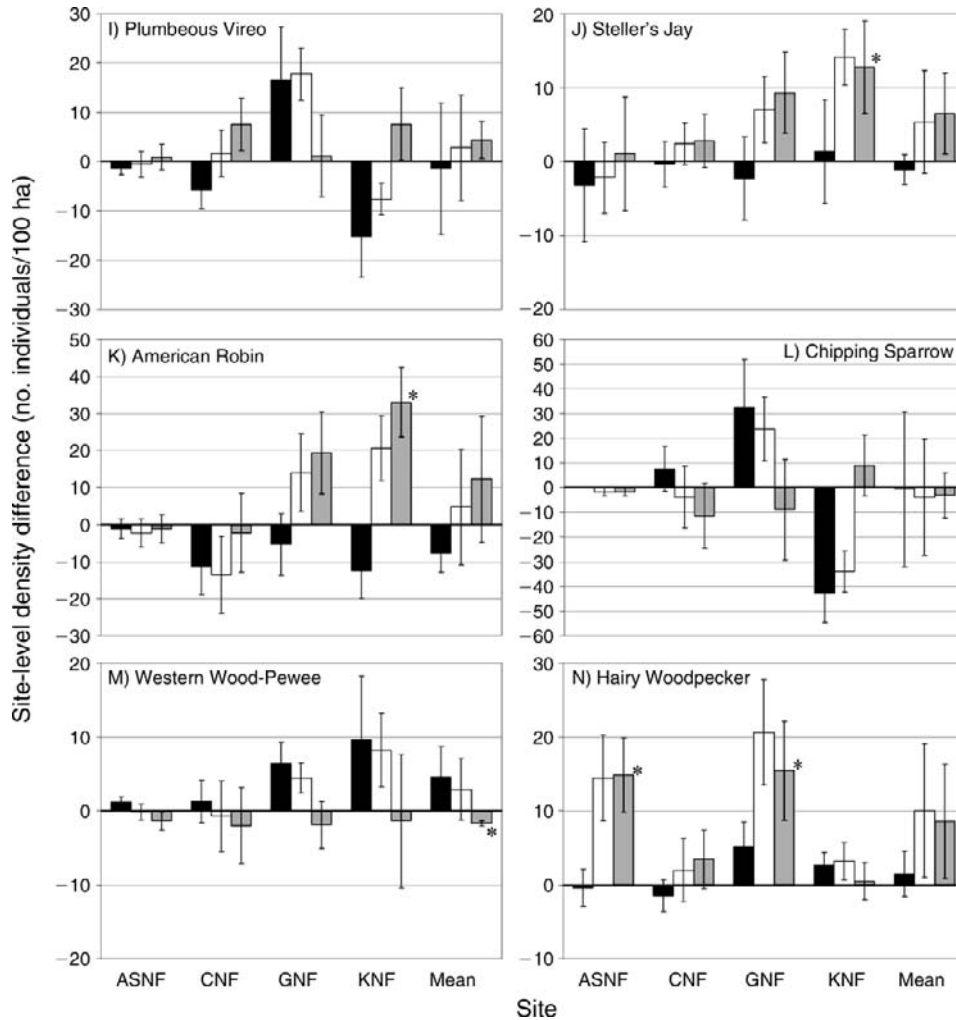


FIG. 2. Continued.

TABLE 2. Model-averaged regression coefficients ($\tilde{\beta}$) and unconditional variance estimates (with SE in parentheses) for habitat variables used to predict the mean point-level response (Δ_i^*) of bird density (individuals/100 ha) to prescribed fire for 14 inference species at four sites in Arizona and New Mexico.

Species	Treatment	Elevation	Slope	PatchType	PatchRich	FAC_1	FAC_2	FAC_3
Dark-eyed Junco	2.45 (6.18)	-1.39 (2.88)	-0.60 (2.75)	0.86 (4.08)	10.87 (9.07)	2.62 (4.36)	-2.42 (4.07)	0.80 (2.98)
Pygmy Nuthatch	-11.12 (8.73)	-2.94 (3.28)	-1.43 (2.93)	9.41 (6.71)	-1.14 (3.34)	1.41 (3.02)	-4.50 (4.07)	2.05 (3.83)
Western Bluebird	6.98 (8.38)	-3.24 (3.52)	0.79 (2.26)	-0.14 (2.75)	0.02 (2.17)	-0.48 (2.02)	-0.18 (1.55)	-2.77 (3.34)
Grace's Warbler	1.12 (4.37)	-12.30 (3.03)	1.57 (2.52)	-0.58 (2.09)	0.62 (2.03)	2.84 (3.24)	-1.19 (2.07)	0.28 (1.39)
Mountain Chickadee	3.74 (6.59)	-2.20 (3.06)	-0.78 (2.43)	7.86 (6.48)	-0.59 (2.86)	15.17 (4.19)	-7.70 (4.31)	-0.35 (2.76)
Western Tanager	0.73 (2.09)	-2.75 (1.68)	-0.93 (1.39)	-1.22 (1.70)	0.09 (0.85)	1.48 (1.68)	-0.36 (0.85)	-0.60 (1.08)
Yellow-rumped Warbler	1.41 (5.77)	-14.92 (4.58)	4.60 (4.70)	-0.68 (3.20)	-2.09 (3.96)	6.70 (5.56)	-2.55 (3.51)	-2.09 (3.24)
White-breasted Nuthatch	-1.64 (3.87)	2.08 (2.46)	1.30 (2.31)	-0.95 (2.60)	-0.60 (2.34)	-0.38 (1.71)	-4.18 (3.20)	-0.12 (1.54)
Plumbeous Vireo	1.18 (3.17)	-2.40 (2.46)	2.60 (2.46)	0.83 (2.14)	-0.60 (1.70)	0.66 (1.61)	-2.49 (2.18)	-0.84 (1.68)
Steller's Jay	3.98 (3.96)	-1.99 (1.89)	0.65 (1.59)	0.61 (2.21)	1.26 (2.24)	-1.23 (1.89)	0.01 (0.84)	-2.11 (2.28)
American Robin	23.19 (6.30)	0.31 (1.74)	-1.50 (2.57)	0.30 (2.95)	0.81 (2.71)	0.79 (2.26)	2.65 (3.39)	3.01 (3.69)
Chipping Sparrow	-2.58 (5.17)	-15.06 (3.45)	3.21 (4.53)	12.77 (8.80)	0.71 (3.10)	4.14 (4.61)	-7.73 (0.05)	-9.05 (5.99)
Western Wood-Pewee	0.09 (1.15)	-0.82 (0.99)	0.38 (0.90)	1.97 (1.99)	2.06 (1.90)	0.06 (0.65)	0.03 (0.64)	0.58 (1.06)
Hairy Woodpecker	5.69 (3.31)	-0.10 (0.72)	1.19 (1.40)	2.39 (2.13)	-0.87 (1.52)	3.24 (1.70)	-0.01 (0.60)	-0.01 (0.91)

Notes: Species are arranged based on greatest to fewest numbers of detections. Variables are as defined in Table 1.

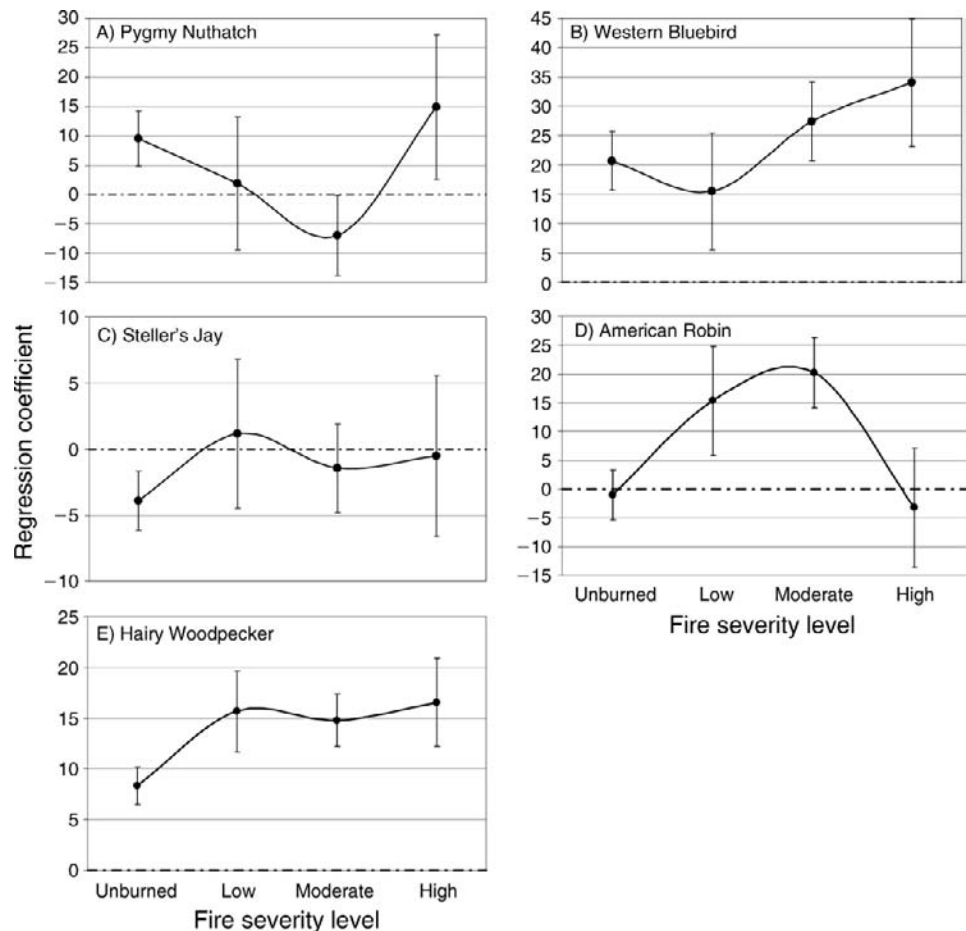


FIG. 3. Regression coefficients ($\hat{\beta}$) for the mean ($\pm$ SE) point-level response ($\hat{\Delta}_i^*$) of avian density (individuals/100 ha) to four levels of fire severity on four study sites in Arizona and New Mexico. Species are arranged (A–E) based on greatest to fewest numbers of detections.

Bluebird, (0.561), and Steller’s Jay (0.642), we were unable to fit a better model than the intercept-only model and regression coefficients indicated a mixed response by these species to fire severity (Table 3). The strong response of the American Robin was best approximated by a second-degree polynomial model and the response of the Hairy Woodpecker (0.866) by the log normal and linear model forms ($\Delta AIC_c \leq 2$ for both). For each of the

five species, no pairwise difference among severity level categories was statistically significant (all P ’s > 0.07).

Overall, we observed little or no spatial structure in residual and semivariance plots of species response to habitat variables or fire severity at the unit level, suggesting that our point-level estimates of density were not highly influenced by spatial correlation in the data. Although the exponential spatial covariance model was

TABLE 3. Values of Akaike’s Information Criterion (corrected for small sample size, AIC_c) and AIC_c differences (ΔAIC_c) for three model forms and an intercept-only (null) model used to predict the mean point-level response ($\hat{\Delta}_i^*$) of five avian species to four levels of prescribed fire severity on four study sites in Arizona and New Mexico.

Model form	Pygmy Nuthatch		Western Bluebird		Steller’s Jay		American Robin		Hairy Woodpecker	
	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
Linear	433.4	1.10	316.8	0.30	50.3	1.60	319.4	4.90	–172.1	0.50
Log normal	432.9	0.60	317.1	0.60	50.2	1.50	318.1	3.60	–172.6	0.00
Polynomial	432.3	0.00	318.6	2.10	52.2	3.50	314.5	0.00	–170.5	2.10
Null	432.5	0.20	316.5	0.00	48.7	0.00	319.9	5.40	–169.2	3.40

Notes: Models used for inference were determined by values of $\Delta AIC_c \leq 2$. Species are arranged based on greatest to fewest numbers of detections.

always the best model of spatial correlation, these models were typically <2 AIC_c of the best nonspatial model.

DISCUSSION

Response of avian species density to prescribed fire treatments

For the 14 species most frequently detected, our analysis revealed few significant differences in pre- and posttreatment density and no species responded strongly to treatment on all four sites. At the site scale, we considered Western Bluebird (trend = +), Plumbeous Vireo (+), Steller's Jay (+), Western Wood-Pewee (−), and Hairy Woodpecker (+) to be consistent fire responders, although the mean response difference for each species was never large ($<|13|$ individuals/100 ha). Because Pygmy Nuthatch had the largest mean response (−18.7), we also considered this species to be a reliable fire responder. The few published studies that examined the short-term response of breeding bird communities to prescribed fire treatment in ponderosa-dominated habitats (e.g., Bock and Block 1983, Horton and Mannan 1988, Hurteau et al. 2008) also reported little or no overall change in density or abundance in most species for which coarse estimates could be generated, including many of those in our inference set. Site-scale differences reported by studies of avifaunal response to wildland fire events, however, were less tractable, and statistical limitations in these studies, coupled with inherent geographical and biological variation in the species under investigation, have tended to produce mixed or conflicting results. Importantly, our inferences relied on estimation methods very different from those of previously published observational studies of wildland fire effects and any generalizations about avifaunal response to fire should be considered with these differences in mind.

Because avifaunal response to disturbance can be a multi-scale process (Brawn et al. 2001), we believe that our site-level results provided an incomplete picture of individual species response to prescribed fire. Our point-level statistical models of species response to treatment, habitat variables, and fire severity revealed mechanistic relationships that were more easily interpreted. In addition, these models allowed us to discriminate between the role of treatment effects and prefire habitat factors at a more meaningful ecological scale. Among the five species that responded to treatment at the point level, only the results for Pygmy Nuthatch suggested a decline in density. Reviews by Kotliar et al. (2002) and Bock and Block (2005a) indicated a negative numerical response by Pygmy Nuthatch to wildland fire, and Dwyer and Block (2000) related this result to moderate levels of wildland fire severity. We agree with Johnson and Wauer (1996) that postfire declines in this species were probably due to the immediate consumption or modification of their primary foraging substrate (e.g., ponderosa pine bark and needles; see Breece et al. 2008). The positive postfire difference in density exhibited by

Western Bluebird in our study is also consistent with results from prescribed (Hurteau et al. 2008) and wildland fires (Bock and Block 2005a) in southwestern forests. Similar to the observations of Dwyer and Block (2000) and Bock and Block (2005b), we detected the largest difference for this species on high-severity points and attribute this increase to improved foraging conditions in these areas. For Steller's Jay, Johnson and Wauer (1996) also observed a generally positive numerical response to wildland fire, although Hejl (1994), Finch et al. (1997), and Bock and Block (2005a) summarized mixed responses. Based on these findings and our point-level analysis, the factors that underlie these results remain unclear.

The results of our experiment indicate that avian response to prescribed fire can be successfully modeled as a function of prefire habitat and fire severity. To our knowledge, no previous studies have used a controlled experiment to relate the response of individual species to prescribed fire-induced levels of severity effects. Of the five species most strongly responding to the treatment variable at the point level, changes in density for only two species could be clearly associated with levels of fire severity. American Robin exhibited the strongest treatment response at both the treatment unit and point scales and increases in density were related to low and moderate levels of fire severity. In their analysis of short-term avian response to wildland fire in mixed-coniferous stands in Montana, Smucker et al. (2005) detected a positive difference in the pre- and postfire (≤ 3 years) relative abundance of American Robin and found that this response was only statistically significant at moderate levels of fire severity. Three years after a large wildfire in northern Arizona, Bock and Block (2005b) reported large numbers of American Robin detections on sampling stations that were moderately burned, although most detections occurred on severely burned stations during the breeding season. The immediate and strong numerical response of this species to levels of fire severity that we observed was probably related to fire-induced effects we did not measure directly, including favorable changes in understory vegetation composition and vigor (Sackett and Haase 1998) and increased food availability (e.g., earthworms, arthropods, and fruits; Short and Negrón 2003).

Hairy Woodpecker also exhibited a strong positive numerical response at treatment unit and point scales. Similarly, Bock and Block (2005a, b) summarized generally positive increases in Hairy Woodpecker abundance in western forests burned by more severe wildland fire. Although the mean point-level difference between pre- and posttreatment density that we estimated was greatest at the highest fire severity level, this difference was not significantly different from the three other levels of severity, including unburned ($\beta = -0.082$, SE = 0.046, Tukey-Kramer $P = 0.349$), and the best functional form (e.g., linear) of this response was not clear. Smucker et al. (2005) reported the response of

Hairy Woodpecker to be statistically significant only for high levels of wildfire severity; however, the estimated difference between high and moderate levels was not statistically significant ($\alpha = 0.05$) and the functional form of this response to four levels of severity was not linear.

We attributed the posttreatment increase in Hairy Woodpecker density to increased food availability and the positive response of fire-dependent arthropod communities (e.g., bark beetles) to higher levels of fire severity and tree mortality (Powell et al. 2002, McHugh et al. 2003, Breece et al. 2008). Across our sites, the bark beetle community (namely, western pine beetle [*Dendroctonus brevicomis* LeConte], southern pine beetle [*D. frontalis* Zimmerman], and *Ips* species) was more abundant and diverse on trees damaged by prescribed fire than on trees located on control units (Breece et al. 2008). Between 2003 and 2005, eight bark beetle species were detected on 105 (10%) of 1045 trees sampled on treatment units, compared with 24 (2%) of 1197 trees sampled on control units. Fifty nine (5%) of the trees sampled on treatment units were presumably killed by bark beetles, compared to only two (0.2%) on the controls. In addition to an increase in the number of trees attacked and killed by bark beetles, we continued to observe an increase in the foraging activities of Hairy Woodpecker and other woodpecker species on the burned units up to four years after treatment (B. G. Dickson, unpublished data).

In the relatively unproductive ponderosa pine forests of the Southwest, avian densities tend to be low and sample sizes insufficient for precise estimation of density. Of the substantial number of detections and species recorded during four breeding seasons, our distance-based approach permitted the estimation of detection probability and density for only 14 of the most frequently detected species. This begs the question: "Are the patterns of individual and cumulative response to prescribed fire treatments that we observed among common species representative of the broader avian community?" There is some evidence that distribution and abundance patterns among common species may be indicative of patterns observed among other members of the species assemblage (Kintsch and Urban 2002, Jiguet and Julliard 2006), although the literature is far from consistent on this finding (Chase et al. 2000). Notably, Dickson (2006) observed little or no change in overall avian community richness, diversity, and similarity in response to the treatments implemented as part of this study. In light of this information, our results can help to guide the conservation of birds and their habitats when treatment strategies also consider the ecological requisites of sensitive species that are less common.

Management and research implications

Because large-scale treatments are expensive and difficult to implement, information on treatment-induced changes to forest structure may be limited or unavailable to most forest managers. If prefire forest

structure attributes are central in determining postfire levels of fire severity (Cocke et al. 2005, Dickson 2006), then predictive models with independent variables that include pretreatment (i.e., initial) habitat conditions can be useful to managers interested in understanding the likely outcomes of prescribed fire treatments on forest attributes, including avifauna, prior to their implementation. As demonstrated by our results, these models can be further improved by the inclusion of covariate information derived at spatial scales that capture relevant ecosystem processes.

Our results suggest that, in the short term, more common members of the breeding bird community that we examined in southwestern ponderosa pine forests are tolerant of prescribed fire treatments at the intensities that we studied (e.g., broadcast burning). In addition, these communities appear able to accommodate these treatments at multiple spatial scales and across multiple geographic locations (Dickson 2006). An important caveat, however, is that the short-term (2-year) post-treatment patterns that we detected could change with time since treatment. Because time since disturbance has been observed to influence results from studies of avian response to fire (e.g., Johnson and Wauer 1996, Smucker et al. 2005), long-term monitoring will be necessary to associate patterns of change with the direct (e.g., tree mortality) and indirect (e.g., increased food availability) effects of fire treatment. Individual-based monitoring efforts may also reveal annual patterns of site fidelity and nest productivity. Nevertheless, short-term studies of wildlife community response to prescribed fire can inform longer-term management objectives when rigorous assessments focus on the immediate periods or seasons during which species might be most affected by treatments (see Rotenberry et al. 1995), and less affected by complex successional trajectories or demographic factors (Johnson and Wauer 1996).

Because forest managers concerned about fire risk, for example, are more likely to implement fire treatments that result in low-to-moderate levels of severity, research should more closely investigate the effects of these treatments on avian populations and habitats. Results from case studies that examine the simple correlation between stand-replacing fire events and avifauna may produce information that is inconsistent and of limited relevance to management needs (Bock and Block 2005a). Thus, robust generalizations about the response (e.g., density) of avifauna to forest management activities, including prescribed fire, will require that research efforts emphasize experiments and the mechanisms underlying observed patterns (Marzluff et al. 2000, Van Horne 2005).

Concomitantly, this interpretation of our results assumes that avifauna in southwestern pine forests are tolerant of low-to-moderate levels of fuels treatments because important habitat features and resources remain after such treatments. However, if these communities occupy habitats that were previously degraded by

human-induced factors, such as logging and fire suppression (Hejl 1994, Hall et al. 1997), then patterns inferred from our results should be tempered by the local or regional influence of these historical activities. Although relatively common on our sites, regional declines in Pygmy Nuthatch, White-breasted Nuthatch, and Western Bluebird, for example, have been attributed to human modification of the landscape since Euro-American settlement (see Hall et al. 1997). Unfortunately, knowledge of presettlement avian community structure and habitat is incomplete and managers lack even rudimentary baseline information (Chambers and Germaine 2003). Our results, coupled with future experiments that investigate avian response to various treatment alternatives on multiple landscapes, will help to fill this knowledge gap.

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APPENDIX A

Predictor variables and scales of association used to model the multi-scale response of avifauna to habitat, prescribed fire, and fire severity at four study sites in Arizona and New Mexico, USA (*Ecological Archives* A019-026-A1).

APPENDIX B

Results from analyses used to quantify the PatchType variable at four study sites in Arizona and New Mexico (*Ecological Archives* A019-026-A2).

APPENDIX C

Methods used to estimate the variance in density difference when $500 < n < 1000$, and to account for stratum-level detection probabilities estimated using the multiple covariates (*Ecological Archives* A019-026-A3).

APPENDIX D

Results from the pretreatment habitat factor analysis using the nine local-scale forest structure variables measured at four study sites in Arizona and New Mexico (*Ecological Archives* A019-026-A4).