



Habitat Relations

Stand Structure and Breeding Birds: Implications for Restoring Ponderosa Pine Forests

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ABSTRACT Fire-adapted forests in the western United States have dramatically departed from the natural or evolutionary environment over the past century because of fire suppression, logging, grazing, and other management practices. In particular, most southwestern ponderosa pine (*Pinus ponderosa*) forests are characterized by dense stands of small-diameter trees that are susceptible to stand-replacing crown fires and ensuing damage to watersheds, wildlife habitat, and communities at the wildland-urban interface. Restoration treatments using mechanical thinning and prescribed fire have become the dominant management paradigm in this forest type, with landscape-scale projects being implemented over the next 20 years. Although many studies have examined wildlife responses to restoration treatments, single-species information is difficult for managers to synthesize and incorporate into management decisions made at large scales. Our goal was to investigate responses of breeding birds in ponderosa pine forests to forest stand characteristics modified by restoration treatments. We sampled birds in 23 stands for 3 years in northern Arizona, and used multi-season and multi-species occupancy models to determine relationships between avian occupancy and stand attributes affected by treatment. Increasing occupancy rates and species richness were associated with decreasing canopy cover, increasing density of mature trees, and increasing density of snags. Occupancy rates and species richness were negatively associated with quadratic mean diameter, medium-sized trees, and downed woody material. Associations of the avian community and individual species with herbaceous cover and tree clumping were less consistent. Our results support the implementation of forest restoration treatments for restoring avian community occupancy in ponderosa pine forests, and emulating the evolutionary environment is likely the best approach. We recommend reducing canopy cover via thinning, and retaining trees >45.7 cm diameter at breast height and snags. A commonly-proposed diameter cap for retaining large trees after thinning (40.6 cm dbh) seems unlikely to benefit nesting passerines, as resulting tree densities would remain too large. We recommend occupancy modeling as an efficient method for assessing wildlife-habitat relationships at large scales. © 2013 The Wildlife Society.

KEY WORDS Arizona, avian community, diameter cap, forest management, habitat relationships, occupancy modeling, *Pinus ponderosa*, ponderosa pine.

In the western United States, over 12 million hectares of conifer forest have co-adapted with fire over a >10,000-year period (Covington 2003). Prior to Euro-American settlement (hereafter presettlement, ca. 1890), frequent fires were the dominant disturbance regime, exerting a strong influence on forest structure and ecosystem function. In southwestern ponderosa pine (*Pinus ponderosa*) forests, low-intensity fires occurred at a 2–25-year return interval (Moore et al. 1999), maintaining a largely open, patchy forest dominated by mature trees and well-developed herbaceous understory (Covington and Moore 1994, Waltz et al. 2003). Because of the patchy spatial and temporal nature of fire, ponderosa

pine trees often grew in uneven-aged clumps (Cooper 1961, White 1985), and snags and downed wood were unevenly distributed on the landscape (Knapp et al. 2005). Following a century of fire suppression, logging, and grazing, ponderosa forests exhibit conditions outside their natural range of variability (Cooper 1960, Covington and Moore 1994, Swetnam et al. 1999). Contemporary ponderosa pine and pine-oak forests are characterized by homogenous, dense stands dominated by small-diameter trees, conditions that facilitate uncharacteristically large and intense stand-replacing crown fires (Fulé et al. 1997, Abella and Fulé 2008).

To reduce threat of wildfire, ecological restoration projects are being implemented in these forest ecosystems. Treatments typically include the use of mechanical thinning and burning to reduce heavy fuel loads, followed by regular application of prescribed fire to approximate the natural fire regime (Moore et al. 1999, 2006b). These treatments are also designed to restore ecosystem function, by increasing rates of

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decomposition and nutrient cycling, water availability, carbon storage, plant biodiversity, and populations of native wildlife species (Allen et al. 2002, Finkral and Evans 2008, Boerner et al. 2009, Schwilk et al. 2009). Understanding treatment effects is particularly important as restoration efforts are implemented at increasingly larger scales (West-erling et al. 2006). For example, the 2010 Collaborative Forest Landscape Restoration Project (Omnibus Public Land Management Act 2009) supports restoration on 9 National Forests across the western United States at scales of 10,000s of hectares. One such project, the Four Forests Restoration Initiative, will treat >400,000 ha of ponderosa pine and pine-oak forest in Arizona alone.

Post-European settlement changes in southwestern forests have significant implications for breeding songbirds, which use a variety of patch types and microhabitats for nesting and foraging. Quantitative studies of avian communities in these forests are relatively recent, so our understanding of presettlement avian communities is limited at best (Block et al. 1997). Similarly, studies of avian responses to forest management have largely focused on silvicultural treatments and commercial harvest (Finch et al. 1997, Kalies et al. 2010). Few studies have explicitly examined avian community responses to restoration treatments (but see Gaines et al. 2007, 2010). Until large-scale, replicated experimental studies are conducted, inferences concerning avian responses to post-settlement changes in forest structure and inversely, restoration, can be derived from extant information on habitat relationships (Block et al. 1997).

We used an extensive, pre-restoration data set to assess avian responses to stand attributes affected by restoration treatments such as tree density, size, and spacing. Because breeding birds in ponderosa pine forests exploit distinct niches (Szaro and Balda, 1979a), we expected both positive and negative associations with alteration of stand structure. We hypothesized that most species would respond positively to attributes characteristic of presettlement forests, for example, open canopy, mature and old-growth trees, clumped tree distribution, large snags, and a well-developed herbaceous understory. We also evaluated 1 stand attribute prominent in current debates over forest restoration practices in the Southwest: the density of large, non old-growth trees. The presumed scarcity and ecological importance of such trees has spurred calls for diameter caps that prohibit cutting of live trees above a certain diameter (typically >40.6 cm) during thinning operations (Allen et al. 2002, Abella et al. 2006). Our specific objectives were to 1) quantify the influence of treatment-affected stand attributes on occupancy rates of individual species and on species richness; and 2) derive inferences from these relationships to inform future restoration of ponderosa pine forests.

STUDY AREA

We sampled avian communities and forest structural characteristics at 23 randomly-selected stands in northern Arizona, which represented existing, pre-restoration con-

ditions within ponderosa pine and ponderosa pine-Gambel oak (*Quercus gambelii*) forest cover types (Fig. 1). Stands in the ponderosa pine cover type had overstory composed of ponderosa pine and herbaceous understory dominated by grasses, primarily Arizona fescue (*Festuca arizonica*) and blue grama (*Bouteloua gracilis*). Pine-oak stands also had a well-developed Gambel oak component that included shrub-like clumps of smaller plants and trees of varying sizes (Rosenstock 1998). Per current United States Forest Service criteria, stands were classified as pine-oak if >10% of tree basal area was comprised of oaks >13 cm in diameter, measured at root collar. Most stands were managed for commercial timber production and had received prior pre-commercial thinning or tree harvest by single-tree selection, group selection, patch-cut, or shelterwood methods. Prescribed fire was commonly applied to reduce woody debris following harvest or thinning treatments. Three stands were research or natural areas not managed for timber production that had a history of natural or prescribed fire. Each stand was ≥ 40 ha in size and had no silvicultural treatment or fire for ≥ 5 years prior to the study.

METHODS

Data Collection

Within each stand, we randomly placed a 2×4 rectangular grid of sampling points spaced 200 m apart, for a total of 184 points in the 23 stands. We conducted bird sampling at the point scale, which is appropriate to the home range size of focal organisms, and also to capture the considerable within-stand variability in forest structure. We used a differentially-correcting global positioning system (GPS) receiver to obtain Universal Transverse Mercator (UTM) coordinates of each point. We surveyed each point for birds $3 \times$ per year, once by each of 3 observers, between 1 June and 31 July, from 1993 to 1995. Surveys occurred during a 3-hour period beginning 30 minutes after sunrise, but not during periods of strong wind or rain. Upon arriving at a point, the observer waited for 3 minutes, and then conducted an 8-minute count of all birds seen or heard within a 100-m radius. We did not count birds flying overhead or detected between points.

We tallied live trees and measured their diameter at breast height in 3, non-overlapping, 0.1-ha circular subplots, 1 centered on the point, the others randomly placed within a 100-m radius. We sampled tree spacing in each subplot, measuring distance from the live tree closest to plot center to the nearest live tree in each of the 4 cardinal directions. We counted all snags within a 100-m radius of the point, excluding those unlikely to provide nesting substrate (<20 cm dbh, displaced >45° from a vertical position, or having extensive fire char and exterior hardening). We sampled understory vegetation and downed woody material at 100-point intercepts, spaced 0.5 m apart on 2 perpendicular transects centered on the point. We measured canopy cover of live trees using a spherical densiometer (Strickler 1959), collecting 5 measurements within each 0.1-ha circular plot, 1 at plot center, and 1 along each of the 4 transect radii 15 m from the center.

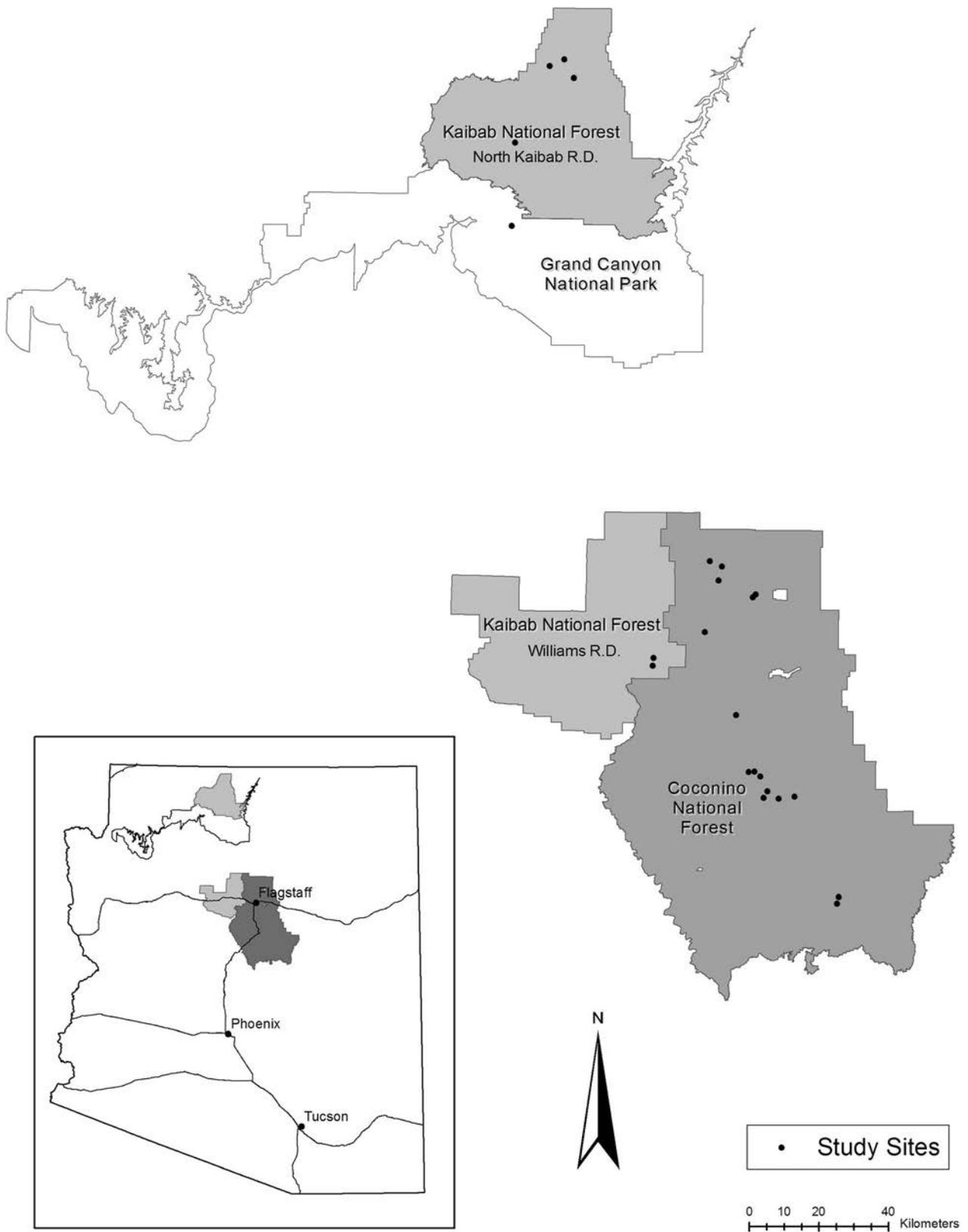


Figure 1. Locations of 23 forest stands sampled for avian occupancy in northern Arizona, 1993–1995.

Data Analysis

We used an occupancy modeling framework that allowed robust estimation of probability of occupancy by individual species, given a suite of covariates expected to influence

habitat suitability and detectability during repeated surveys (MacKenzie et al. 2006). For each point, we quantified overstory and understory characteristics using variables commonly used to describe stand structure and that

Table 1. Summary statistics for habitat covariates measured at each site ($n = 182$) in northern Arizona, 1993–1995.

Habitat covariate	Min.	Max.	Median	Average	SD	Covariate name used in text
Ponderosa pine canopy cover (%)	14.9	72.5	47.5	47.2	13.0	Canopy cover
Ponderosa pine quadratic mean diameter (cm) ^a	10.1	47.7	26.7	27.5	7.9	QMD
Number of medium-sized (40.6–45.7 cm dbh) ponderosa pine trees/ha ^b	0.0	43.3	10.0	11.1	9.2	Cap trees
Number of large (>45.7 cm dbh) ponderosa pine trees/ha ^c	0.0	113.2	20.0	27.2	23.1	Large trees
Clark and Evans (1954) spacing index ^d	0.6	1.8	1.1	1.1	0.2	Tree spacing
Number of snags/ha ^e	0.0	50.9	3.5	5.4	5.8	Snags
Downed woody material cover (%)	1	62	15	18	11	Downed woody material
Grass and forb cover (%)	1	100	36	38	22	Herbaceous cover
Forest cover type ^f (binary)	0 (binary)	1 (binary)				Forest cover type
UTM nothing	4069675	3824212	3895705	3917654	78101	Latitude

^a The diameter of the tree of average basal area (Curtis and Marshall 2000).

^b 40.6 cm (16 inches) is the common cut-off point for socially-based diameter caps in the Southwest (Abella et al. 2006).

^c Definition reflects current U.S. Forest Service management strategy for southwestern ponderosa pine forests (Reynolds et al. 1992, Youtz et al. 2008).

^d Measure of spacing (R) among individual ponderosa pine trees (>40.6 cm dbh). $R > 1$ indicates uniformity, $R = 1$ indicates a random distribution, and smaller values represent increasing aggregation, with maximum at $R = 0$.

^e Including ponderosa pine and Gambel oak snags.

^f Ponderosa pine = 0, ponderosa pine–Gambel oak = 1.

potentially influence avian occupancy. We diagnosed univariate correlations using a Pearson correlation matrix, and omitted variables correlated at >0.60 . The remaining variables used in our analysis (hereafter, habitat covariates; Table 1) included percent canopy cover of ponderosa pine (canopy cover); ponderosa pine quadratic mean diameter (QMD; cm); density of medium-sized (40.6–45.7 cm dbh) ponderosa pines, to simulate a diameter cap (cap trees); density of mature and old growth ponderosa pine (>45.7 cm dbh; Youtz et al. 2008; large trees); spatial aggregation of ponderosa trees, using the Clark and Evans (1954) index (tree spacing); density of snags; percent cover of downed woody material; and percent cover of herbaceous understory (Table 1). Because forest cover type has a strong influence on breeding birds (Rosenstock 1998), we included a binary variable classifying each stand as ponderosa pine (0) or pine–oak (1; see Study Area). Finally, we used the UTM nothing coordinate (latitude) of the stand center as a surrogate for unmeasured habitat variables (Rahbek and Graves 2001) and to account for expected latitudinal differences in avian community composition.

We hypothesized that percent canopy cover, year, and survey number within a year could cause heterogeneity in detection, colonization, or extinction probability. Canopy cover can obscure birds both visually and audibly, reducing detection probabilities in dense stands. Year and survey number can capture variability in weather and other attributes that are difficult to measure (e.g., changing resource availability), all of which can affect animal behavior and detectability (Karplus 1952). Observer effects also influence bird detection during surveys (Link and Sauer 1998). We attempted to control this variable by carefully selecting and training observers and allocating survey effort equally across them, rather than include observer as a detection covariate. We controlled time and weather-related effects by limiting surveys to a 3-hour period beginning 30 minutes after sunrise and days without strong wind or rain. We standardized all continuous habitat and detection covariates.

We first analyzed data for each species in a multi-season framework MacKenzie et al. (2003, 2006), estimating detection probability (p), the probability of detecting each species at a point if it was present; occupancy (ψ), the expected probability that a given point was occupied; colonization (γ), the probability that an unoccupied point was occupied in the following season; and local extinction (ϵ), the probability that an occupied point was unoccupied in the following season. If multi-season models were over-parameterized (i.e., insufficient points for the number of detections) as indicated by large standard errors, we substituted single-season models (MacKenzie et al. 2002, 2006). In these cases, we treated each point and year as an independent observation and used year as a detection covariate.

We used all combinations of covariates to identify the most parsimonious models of detection, extinction, and colonization. We then applied an all-subsets approach to assess influence of habitat covariates on occupancy by each species. We constructed these models ($n = 1,024$ per species) using the RMark package (Laake 2011) in R (R Development Core Team 2011). For each model, we computed Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and Akaike weights (w_{ij} , weight of covariate i for species j ; Burnham and Anderson 2002), and used these values to assess model fit. We ranked relative covariate importance by summing w_{ij} across all models in which a given covariate occurred and used cumulative weights to rank relative covariate importance for each species. Larger values of w_{ij} are indicative of greater importance for covariate i relative to other variables in the model (Burnham and Anderson 2002). We considered $w_{ij} \geq 0.50$ indicative of a strong occupancy response to the covariate and $w_{ij} < 0.50$ a weak response. For each covariate, we averaged w_{ij} across species to estimate overall importance (Dickson et al. 2009). We also calculated model-averaged parameter ($\hat{\beta}_j$) estimates and unconditional standard errors (SE) for each habitat covariate to assess the direction of response by each individual species and the collective group

of species. We included forest cover type and latitude in the models, to account for these influential sources of heterogeneity, but because of convergence problems with these parameters in some models, we did not attempt to interpret their averaged w_{ij} weights relative to other covariates. We do not expect that these problems with convergence affect our interpretation, since we are only interested in the relative importance of variables rather than estimates of effect sizes.

To examine patterns of species richness, we used a multi-species hierarchical model that estimated individual species occurrences, while accounting for imperfect detection of species (Dorazio et al. 2006, Zipkin et al. 2010), thus allowing us to remain consistent with our single species occupancy models. We analyzed the model using methods of data augmentation, which allows for estimation of the number of species in the community not detected during sampling (Royle et al. 2007, Kéry and Royle 2009). We ran the model in a Bayesian framework using programs R and WinBUGS (Spiegelhalter et al. 2003) following the approach of Zipkin et al. (2010). We ran 2 chains of length 20,000 with a burn-in of 5,000 and thinned the posterior chains to 10. We estimated point-level species richness as a function of all continuous habitat covariates and year as a detection covariate, in a single-season modeling framework. We excluded forest cover type as a covariate, because a number of species occurred only in the pine–oak type, causing the model to fail to converge. Visual examination of modeled versus observed species richness suggested that omission of this covariate did not affect our results. As in

Zipkin et al. (2010), the model does not build in explicit relationships between point-specific richness and covariates; thus, we estimated richness at each point and determined the direction of the response of species richness versus each covariate.

RESULTS

We sampled all 184 points in each of 1993, 1994, and 1995, losing only 8 points in the last survey of 1995 because of inaccessibility. We detected 48 species, and obtained 12,848 total detections (Appendix A, available online at www.onlinelibrary.wiley.com).

We developed multi-season occupancy models for 14 species and single-season models for 2 additional species (yellow-rumped warbler [*Setophaga coronata*] and Steller's jay [*Cyanocitta stelleri*]; Appendix B). All 16 species had detection probabilities >0.20 , adequate for building robust occupancy models (MacKenzie et al. 2006). Western bluebirds (*Sialia mexicana*) and broad-tailed hummingbirds (*Selasphorus platycercus*) had >300 detections but occupancy rates approaching 1.0 (>0.95), precluding reasonable models of occupancy (MacKenzie et al. 2003). The remaining species had detection probabilities <0.20 and could not be modeled individually using these methods.

For the 16 species, habitat covariates associated with occupancy (most to least important, based on average w_{ij}) were QMD, downed woody material, canopy cover, herbaceous cover, snags, large trees, cap trees, and tree spacing (Table 2). All covariates except cap trees and tree spacing had a strong association with species' occupancy.

Table 2. Cumulative Akaike's Information Criterion (AIC) weights (w_{ij}) for assessing the relative importance of habitat covariates used to predict occupancy of bird species, and averaged over the community, followed by the direction of the response in parenthesis as indicated by model-averaged parameter ($\hat{\beta}_j$) estimates. Values of $w_{ij} \geq 0.50$ (*) indicate strong evidence for a species response to the habitat covariate. The last row presents the direction of response of each habitat covariate in the species richness model.

Species	Scientific name	Total detections	Canopy cover	QMD ^a	Cap trees ^b	Large trees ^c	Tree spacing ^d	Snags	Downed woody material	Herbaceous cover
Pygmy nuthatch	<i>Sitta pygmaea</i>	2,058	0.98* (–)	1.00* (–)	0.35 (–)	0.76* (+)	0.27 (+)	0.73* (+)	0.84* (–)	0.66* (–)
Dark-eyed junco	<i>Junco hyemalis</i>	1,504	0.87* (–)	0.98* (–)	0.38 (–)	0.41 (+)	0.37 (+)	0.80* (+)	0.84* (–)	0.59* (–)
Plumbeous vireo	<i>Vireo plumbeus</i>	737	0.83* (–)	0.98* (–)	0.64* (+)	0.46 (+)	0.48 (–)	0.64* (–)	0.54* (–)	0.33 (–)
Grace's warbler	<i>Setophaga graciae</i>	709	0.35 (+)	0.29 (–)	0.34 (+)	0.95* (+)	0.55* (+)	0.31 (+)	0.27 (–)	0.31 (–)
Yellow-rumped warbler	<i>Setophaga coronata</i>	628	0.95* (–)	0.24 (–)	0.30 (–)	0.29 (+)	0.24 (–)	0.50* (+)	0.94* (+)	0.52* (+)
Mountain chickadee	<i>Poecile gambeli</i>	621	0.67* (–)	0.97* (–)	0.29 (+)	0.40 (–)	0.29 (+)	0.57* (+)	1.00* (–)	0.46 (–)
White-breasted nuthatch	<i>Sitta carolinensis</i>	604	0.86* (–)	0.89* (–)	0.40 (–)	0.60* (+)	0.52* (–)	0.83* (+)	0.82* (–)	0.64* (–)
Western tanager	<i>Piranga ludoviciana</i>	549	0.34 (–)	0.66* (+)	0.30 (+)	0.59* (–)	0.29 (+)	0.32 (–)	0.68* (–)	0.79* (–)
Northern flicker	<i>Colaptes auratus</i>	487	0.28 (–)	0.33 (–)	0.54* (–)	0.43 (+)	0.36 (–)	0.96* (+)	0.61* (–)	0.35 (–)
Steller's jay	<i>Cyanocitta stelleri</i>	452	0.39 (+)	1.00* (+)	0.49 (–)	0.70* (+)	0.32 (–)	0.31 (+)	0.05 (–)	0.92* (–)
Violet-green swallow	<i>Tachycineta thalassina</i>	385	0.30 (–)	0.29 (–)	0.73* (–)	0.78* (+)	0.33 (–)	0.37 (+)	0.49 (+)	0.80* (+)
Red crossbill	<i>Loxia curvirostra</i>	366	0.91* (–)	0.97* (–)	0.44 (+)	0.31 (–)	0.92* (+)	0.49 (+)	0.66* (–)	0.53* (–)
Western wood-pewee	<i>Contopus sordidulus</i>	345	0.32 (+)	0.46 (–)	0.58* (+)	0.31 (+)	0.27 (–)	0.71* (+)	0.29 (–)	0.28 (–)
Hermit thrush	<i>Catharus guttatus</i>	286	0.27 (–)	1.00* (–)	0.30 (–)	1.00* (+)	0.27 (+)	0.47 (–)	0.72* (+)	0.33 (–)
Chipping sparrow	<i>Spizella passerina</i>	229	0.30 (+)	1.00* (+)	0.26 (–)	0.64* (–)	0.72* (+)	0.70* (–)	0.63* (+)	0.71* (+)
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	133	0.99* (+)	1.00* (+)	0.96* (–)	0.38 (–)	0.17 (–)	0.41 (+)	0.99* (–)	1.00* (–)
Occupancy average			0.60*	0.75*	0.46	0.56*	0.40	0.57*	0.65*	0.58*
Species richness			(–)	(–)	(–)	(+)	(–)	(+)	(–)	(+)

^a Ponderosa pine quadratic mean diameter (cm).

^b Number of medium-sized (40.6–45.7 cm dbh) ponderosa pine trees/ha.

^c Number of large-sized (>45.7 cm dbh) ponderosa pine trees/ha.

^d Smaller values indicate more clumped tree distributions; greater values indicate even spacing. Thus, a negative response to this variable is a positive response to clumping, for descriptive purposes.

Most species had a positive association with large trees and snags, and a negative association with canopy cover, QMD, cap trees, downed woody material, and herbaceous cover (Table 2). Half the species were positively associated with tree spacing and half negatively (Table 2). Although we did not attempt to interpret the importance of forest cover type, relative to the other variables, all species except for 2 (yellow-rumped warbler and Steller's jay) were positively associated with the presence of Gambel oak (Appendix B, available online at www.onlinelibrary.wiley.com). Finally, for latitude, the direction of association was not as important as using this variable to account for spatial variation in species occupancy; we would expect that some species are found in more northern habitats and some in more southern.

In the species richness model, habitat covariates positively associated with occupancy were large trees, herbaceous cover, and snags; covariates negatively associated with occupancy were canopy cover, QMD, cap trees, tree spacing, and downed woody material (Table 2).

DISCUSSION

Southwestern ponderosa pine forest overstory has little compositional variation; therefore, the relatively small component of Gambel oak provides critical foraging and nesting microhabitats provided by oak trees of various growth forms (1979*b*; Wightman et al. 2007). Consistent with the literature (Brawn and Balda 1988, Rosenstock 1998, Jentsch et al. 2008), we found that most avian species' occupancy was positively associated with the presence of Gambel oak. Loss of oak from fuelwood harvesting in southwestern forests has not been quantified but is a management concern (Abella and Fulé 2008).

Structural attributes of forests are directly affected by thinning, and we found that many such attributes had strong associations with species occupancy of the breeding bird community in our study stands. Most bird species (11/16; 7 strongly) were negatively associated with canopy cover, and overall species richness was negatively associated. In addition, most bird species (11/16 species; 6 strongly) were positively associated with the density of large trees, and species richness was positively associated. In contrast, cap tree density had a negative association with most species (11/16; 4 strongly) and species richness, reflecting low avian diversity and abundance in stands dominated by medium-sized ponderosa pines that also had minimal horizontal or vertical heterogeneity. Critics of diameter caps have noted that size thresholds are arbitrary and lack scientific support (2006*a*). Moreover, caps can reduce within-stand diversity and create post-treatment stand structure considerably different from the evolutionary environment of ponderosa pine forests (Abella et al. 2006). We also detected a negative association with QMD by most species (12/16; 7 strongly), and a negative association with species richness. Although the negative association with QMD seems contradictory to overall positive associations with mature and old-growth trees, QMD values were skewed downward by the preponderance of small diameter trees and relative scarcity of large, old trees in our study stands (average QMD across

all stands was 27.5 cm). Although widely used for forest inventory purposes (Curtis and Marshall 2000), our results suggest that QMD is not well suited for describing the habitat value of large trees to nesting songbirds, due to difficulties in its interpretation.

We found an overall positive association between snag density and bird species richness. Snags were strongly associated with occupancy of species (11/16; 6 strongly), particularly of cavity-nesters, which is a relationship well documented in previous studies of breeding birds in ponderosa pine forests (Cunningham et al. 1980). Our final analysis included 5 cavity nesters: pygmy nuthatch (*Sitta pygmaea*), white-breasted nuthatch (*Sitta carolinensis*), mountain chickadee (*Poecile gambeli*), and northern flicker (*Colaptes auratus*), all of which were strongly associated with snags; and violet-green swallow (*Tachycineta thalassina*), which was weakly associated with snags. The western bluebird and other woodpecker (*Melanerpes, Picoides*) species likely would have demonstrated similar relationships, had they been included among the final models; other studies have reported positive responses to restoration treatments by these species (Wightman and Germaine 2006, Hurteau et al. 2008).

The only variable that clearly had a consistently opposite relationship with occupancy than we hypothesized was downed wood. Most species (12/16; 8 strongly) and species richness had a negative association with downed woody material. Most downed wood in our study stands was comprised of boles and branches from small diameter (<20 cm) pines felled by natural mortality or during pre-commercial thinning operations; materials that would be relatively ephemeral under a more natural, frequent-fire regime. However, we caution that our sampling approach for downed woody material was designed to measure fuels (materials >5 cm diameter), not wildlife habitat per se. Thus, we could not distinguish between large logs and other woody structures providing foraging or nesting microhabitats and responses of species that use them (e.g., house wren [*Troglodytes aedon*]).

Two habitat covariates had opposite relationships with species richness than with the majority of species occupancy results. Most species (13/16; 8 strongly) exhibited a negative association with herbaceous cover, a primary feature of presettlement ponderosa pine forests (Covington and Moore 1994). However, overall species richness was positively associated with herbaceous cover. This may be because only 1 species in the final model set (dark-eyed junco [*Junco hyemalis*]) nests and forages on the ground, but we assessed more ground-dwelling species using the species richness model. Although other studies in these forests (e.g., Rosenstock 1996) have not reported significant correlations between understory variables and breeding birds, we caution that herbaceous cover may influence less-studied species, as well as other wildlife (Kalies et al. 2012). Species richness and half the modeled species (8/16; 3 strongly) responded positively to clumping (i.e., negatively to tree spacing) of ponderosa pine trees, another common though not ubiquitous feature of presettlement forests in the Southwest (Abella

and Denton 2009). This weak relationship by many species likely reflected the relatively high tree density and uniform distribution in our study stands. Well-defined clumps of mature and old-growth trees, like those reported by White (1985) were uncommon. Where present, these groups typically had numerous younger trees embedded within that also were included in our spacing metric. In general, although we were able to assess species' associations with individual attributes of the evolutionary environment of ponderosa pine forests, these components rarely occurred together in our study stands.

Overall, our findings are consistent with previous studies of breeding birds in managed and old-growth ponderosa pine forests (Szaro and Balda 1986, Block et al. 1997, and references cited therein). Although we were able to explicitly model only a third of the breeding avifauna detected during surveys, the species richness results indicate that most other species would also benefit from restoration treatments designed to create conditions resembling the evolutionary environment of southwestern ponderosa pine forests. The single relationship that does not match that expected in the evolutionary environment is the negative association between birds (individually and collectively) to downed woody material, which we caution may be a sampling artifact. In addition, even if perfectly restoring the evolutionary environment was possible, this approach would not benefit every single species. Some songbird species (e.g., western wood-pewee [*Contopus sordidulus*] and black-headed grosbeak [*Pheucticus melanocephalus*]) likely have benefitted from post-settlement changes in ponderosa pine forests, particularly increased tree density and canopy cover (Brawn and Balda 1988), and thus might respond negatively to restoration treatments. Since all of these species are abundant, widely distributed, and lack special conservation status (i.e., are not listed as threatened or endangered), we consider this an acceptable tradeoff to restore ecosystems outside their range of natural variability and at risk of further degradation from stand-replacing crown fires. The inherent natural heterogeneity of ponderosa pine forests suggests that a variety of restoration treatments may best meet conservation objectives and minimize risk of failure as managers undertake the considerable challenge of landscape-scale forest restoration (2006a).

Large-scale implementation of forest restoration treatments necessitates a habitat-focused; multi-species approach to monitor wildlife responses (Lambeck 1997, Lindenmayer et al. 2002). Occupancy modeling is suited for such applications and gaining popularity. In our study, however, we were only able to fit models for about half of the species reasonably well-detected (i.e., >60 total detections) during surveys. Although the number of species we modeled was similar to that of other avian studies of comparable spatial and temporal scale (e.g., Kotliar et al. 2007, Dickson et al. 2009), our inability to model additional species was likely due to low detection probabilities for some species, widespread generalist species that occurred at nearly all sampling points, and the large sample size required when fitting multi-season models with a large set of habitat covariates. Although

conducting more surveys would have increased the number of rare species we were able to model, we had to consider the tradeoff between modeling rare species and over sampling more common species. Thus, the implementation of the species richness model was a good compromise, in that we kept our sampling at a manageable level of effort yet could still draw conclusions at the community level.

MANAGEMENT IMPLICATIONS

Restoration treatments that return southwestern ponderosa pine forests to conditions within their natural range of variability will likely benefit a substantial portion of the breeding songbird community. Tree size and species should be considered when undertaking thinning operations. We recommend retaining ponderosa pine trees >45.7-cm diameter at breast height, Gambel oaks, and snags. The commonly advocated 40.6-cm (16 inches) diameter cap may not benefit breeding songbirds and begs further evaluation for potential adverse effects to other wildlife species. Downed woody material provides habitat for other forest wildlife species such as small mammals; the negative association reported here should be interpreted with caution, especially given constraints of our sampling design. We recommend occupancy modeling (both at the species and community level) as an efficient method for assessing wildlife-habitat relationships at large scales.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

APPENDIX A. All avian species detections.

APPENDIX B. Model-averaged beta estimates and SE for each habitat (occupancy) covariate and species.