

Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire

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Abstract. Prescribed fire is a management tool used to reduce fuel loads on public lands in forested areas in the western United States. Identifying the impacts of prescribed fire on bird communities in ponderosa pine (*Pinus ponderosa*) forests is necessary for providing land management agencies with information regarding the effects of fuel reduction on sensitive, threatened, and migratory bird species. Recent developments in occupancy modeling have established a framework for quantifying the impacts of management practices on wildlife community dynamics. We describe a Bayesian hierarchical model of multi-species occupancy accounting for detection probability, and we demonstrate the model's usefulness for identifying effects of habitat disturbances on wildlife communities. Advantages to using the model include the ability to estimate the effects of environmental impacts on rare or elusive species, the intuitive nature of the modeling, the incorporation of detection probability, the estimation of parameter uncertainty, the flexibility of the model to suit a variety of experimental designs, and the composite estimate of the response that applies to the collection of observed species as opposed to merely a small subset of common species. Our modeling of the impacts of prescribed fire on avian communities in a ponderosa pine forest in Washington indicate that prescribed fire treatments result in increased occupancy rates for several bark-insectivore, cavity-nesting species including a management species of interest, Black-backed Woodpeckers (*Picoides arcticus*). Three aerial insectivore species, and the ground insectivore, American Robin (*Turdus migratorius*), also responded positively to prescribed fire, whereas three foliage insectivores and two seed specialists, Clark's Nutcracker (*Nucifraga columbiana*) and the Pine Siskin (*Carduelis pinus*), declined following treatments. Land management agencies interested in determining the effects of habitat manipulations on wildlife communities can use these methods to provide guidance for future management activities.

Key words: composite analysis; fuel treatments; hierarchical Bayes; point count survey; ponderosa pine; presence-absence data; species richness; WinBUGS.

INTRODUCTION

Land management agencies are increasingly faced with the challenge of quantifying the impacts of management practices (such as fuel reduction programs) on wildlife communities. Species diversity and richness measures are often used as indices to quantify the success of management practices, the extent of human disturbance on ecosystems, or to prioritize the selection of sites for conservation purposes (Waltert et al. 2004, Arponen et al. 2005, Schmidt et al. 2005, Mauro et al. 2007, Veech and Crist 2007). Though assessing impacts

on entire communities is important (Boulinier et al. 1998), land managers must also be able to assess changes in populations of threatened, rare, or endangered species in response to environmental changes. Addressing both issues can be a daunting task for agencies faced with a variety of competing demands on both their time and money. We present an example of an analysis of standard point count data using advanced statistical models that allow the user to assess community-level questions such as turnover and extinction rates, estimate the effect of an environmental change (in this case prescribed fire) on individual species, and generate a composite estimate of the effect of fire treatments on the entire community of species.

In recent years, increasing interest in assessing biodiversity by estimating individual species' occupancy rates, has led to advances in statistical techniques for evaluating species richness and community structure

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(Dorazio et al. 2006, Royle and Kéry 2007, Kéry and Royle 2008a, b). When sampling wildlife populations, many authors assert the importance of estimating probabilities of detection for individuals and species (Nichols 1992, Buckland et al. 2001, Williams et al. 2002, Kéry and Schmid 2006, MacKenzie et al. 2006). However, wildlife researchers often ignore differences in detection probabilities among species during analyses due to inappropriately designed studies or to the complexity of analytical techniques. Incorporating detection probabilities into estimates of species richness is important for obtaining accurate counts of species numbers particularly in communities with large numbers of rare or elusive species (Kéry et al. 2008b). In a series of research papers, models were developed to estimate community-level species richness while accounting for imperfect detection and using information from all species detected regardless of the number of detections for each species (Dorazio et al. 2006, Royle and Kéry 2007, Kéry and Royle 2008a, b).

Prescribed fire is a management practice currently being used by land management agencies to reduce fuel loads and potentially diminish the frequency and intensity of wildfires. Recent legislation regarding postfire management policy (i.e., National Fire Plan [U.S. Department of Agriculture 2000], Healthy Forest Initiative, Healthy Forest Restoration Act [U.S. Department of Agriculture 2003]) focuses forest managers' efforts on reducing the risk of severe wildfires. However, relatively little is known regarding the effects of prescribed fire on breeding bird populations. Prescribed fire may have detrimental effects on species by removing understory vegetation or may create habitat for fire associated species such as cavity-nesting birds (Bock and Block 2005, Saab et al. 2005).

Currently, assessments of avian responses to environmental disturbances, such as fire, are often made by summarizing individual species responses (Bock and Block et al. 2005, Saab et al. 2005, Smucker et al. 2005, Kotliar et al. 2007) or using ordination techniques such as redundancy analysis and detrended correspondence analysis (Morisette et al. 2002, Cleary et al. 2007). Researchers attempting to identify individual bird species-habitat relationships in forests with and without fire often cannot assess populations of rare or elusive species, and generally limit their analyses to species with some minimum number of detections (Morisette et al. 2002, Smucker et al. 2005, Sallabanks et al. 2006, Schwab et al. 2006, Kotliar et al. 2007). However, less common species may be of most interest to land managers. The use of hierarchical models for conducting composite analyses of community response allows for the efficient use of survey data, not just data obtained on a few common species, and does not require the user to make determinations on a species by species basis regarding the minimum sample size required to perform the analysis.

Previous studies evaluating the effects of fire on avian communities have concluded that bird responses vary with fire severity (Bock and Block 2005, Saab et al. 2005, Kotliar et al. 2007). Saab et al. (2005) summarized responses of birds to fire in the Rocky Mountains and concluded that though several species were consistently present in recently burned forests, and other species were consistently more common in unburned forests, most species displayed mixed responses to fire. Differences in burn severity, time since fire, and total burn area between studies was likely the cause of inconsistent responses (Saab et al. 2005). The majority of these studies have been conducted on avian responses to wildfire, rather than experimental application or prescribed fire. Due to the dependency of bird responses to fire severity, effects of prescribed fires on bird communities may differ from the effects of wildfire. Low-severity fire, such as prescribed fire, generally consumes the ground-layer vegetation and duff without killing large overstory trees, while leaving the structure of the dominant vegetation intact (Saab and Powell 2005). In contrast, high-severity fires cause changes in forest structure by killing the above-ground vegetation (Smith et al. 2000). In 2002, we began a before-after-control-impact (BACI) study (Green 1979, Stewart-Oaten et al. 1986) to evaluate the effects of fuels reduction on habitats and populations of birds in ponderosa pine forests throughout the Interior West.

We used a hierarchical Bayesian (HB) multispecies site occupancy model (Dorazio et al. 2006, Kéry and Royle 2008a, b) to assess the community-level impacts of the prescribed fire experiment, and to make inferences about the effects of fire for all species observed in the sample. Here we extend the model of Kéry et al. (2009) to allow for explicit occupancy dynamics and to quantify the effect of prescribed fire treatments on occupancy rates of individual species. The model allows for estimation of occupancy and detection rates for each individual species, incorporation of site- and species-level covariates, and approximation of the uncertainty associated with parameter estimates. Accounting for the probability of detecting a species is critically important. Differences in calling rates, plumage, foraging behavior, and habitat use result in detection probabilities that differ by species. Studies that neglect to account for detection probability will have a sample that over-represents species that are the easiest to detect, which will bias the estimation of population and community attributes (e.g., Nichols 1992, Buckland et al. 2001, Williams et al. 2002, MacKenzie et al. 2006).

An important advantage of the multispecies model is the hierarchical structure, which affords increased precision of estimators due to the sharing of information across species. That is, hierarchical models provide a framework for carrying-out so-called "composite analyses" of data on many species (Sauer and Link 2002). Formulation of the problem as a multi-species occupancy model allows the calculation of species richness and/or occupancy on multiple scales such as plots,

survey unit (treatments), and study areas (Kéry and Royle 2008b). Formulating management guidelines for every individual species is not always a viable option (Franklin 1993, Sallabanks et al. 2006). Therefore, a model which provides land managers with information on which species respond in a comparable manner to habitat changes is a useful tool.

Unlike Kéry et al. (2009), we use the occupancy models to estimate summaries of the observed community size rather than formally estimating the number of unobserved species in the community. In effect, we use the model to adjust sample statistics based on the total number of species observed. Thus, a species may appear in one stand but not another, and we use the models to account for the potential that it was present but not detected in the latter. We did not account for hypothetical un-named species which were not observed because we feel that conclusions about effects of management actions based on such species would be difficult to use in support of management policy.

Avian responses to fire: predictions

On our study sites in Washington, Saab et al. (2006) documented an increase (+28.6%) in large snag (>23 cm) numbers following prescribed fire treatments. Increases in the availability of snags for nesting (Raphael and White 1984) as well as increases in food resources for bark- and wood-foraging species such as Hairy (*Picoides villosus*), Three-toed, and Black-backed Woodpeckers should result in higher densities of these species (McCullough et al. 1998, Hoyt and Hannon 2002, McHugh et al. 2003, Sullivan et al. 2003, Saab et al. 2007).

Live stem numbers and downed woody material declined on our study sites following prescribed fire treatments (Saab et al. 2006). As a result, we expect that postfire populations of shrub nesting birds and foliage gleaners will be reduced until shrub regrowth occurs. Reduced ground cover, however, may benefit granivores and other ground-feeding species (Bock and Lynch 1970, Blake 1982, Dickson et al. 1995). More open canopies that result from fire have been associated with increased populations of aerial insectivores (Kotliar et al. 2002). Open canopies provide room for maneuvers of aerial insectivores and ground-feeding species may benefit from reductions in forest litter after fire (Dickson et al. 1995).

We hypothesize that fuel reduction treatments that result in an increase in snag numbers, a decrease in shrub and ground cover, and a more open canopy will result in increases of bark-gleaning, aerial (possibly including hummingbirds), and ground feeders, while foliage-gleaning and shrub nesting birds will decline in response to prescribed fire.

METHODS

Study area description

Six study units totaling 2107 ha were selected in a 51.5 km long and 29 km wide portion of the Methow

Valley of the Okanogan-Wenatchee National Forest in Washington, USA. All study units were located within ponderosa-pine-dominated (*Pinus ponderosa*), dry, mixed-conifer forest in north-central Washington east of the Cascade Range. Study sites were chosen from a pool of 13 units that were scheduled for imminent operational prescribed burns by the Forest Service. We selected our six study sites based on adequate size (around 325 ha), accessible terrain (e.g., not too steep and rocky for safe field work), and relatively similar vegetation composition and pattern that was representative of dry forest conditions in the area. The six sites were matched in three pairs. One study-site pair was formed by splitting a large area into control and burned units. Another study-site pair combined two units that were 2.5 km apart, and the third pair was formed by combining several small contiguous units into control and burned units. The three study sites to be burned were chosen randomly within each of the three study-site pairs. Understory vegetation was a variable mixture of grasses, forbs, and shrubs. Dominant plant species including snowberry (*Symphoricarpos albus*), spirea (*Spirea* spp.), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus* spp.) (Saab et al. 2006). Prescribed fire on these study sites was designed to reduce existing fuel loads, including surface and ladder fuels, reduce understory tree densities (trees $\leq$ 15.4 cm dbh), and create small gaps in the upper tree canopy, while retaining large pine trees and snags (>23 cm dbh) (M. Dunn, K. Busse, and M. Trebon, *unpublished manuscript*). In the spring of 2004, prescribed fire treatments were implemented on two units and a third unit was burned in the spring of 2005, resulting in three burn units and three controls. Resulting vegetation changes are described in detail in Saab et al. (2006). On these sites, downed woody material declined by 50%, live stems declined overall by 31% with no change in large (>23 cm dbh) stem densities, and large snag densities (>23 cm dbh) increased by 28.5%, with overall snag densities doubling. Average composite burn index ranged from a low of 0.50 ± 0.05 (mean $\pm$ SE) on one study unit to 0.60 ± 0.06 , indicating that all three sites burned at a relatively similar intensity in the low to moderate range of severity.

Field methods

In 2002, we established 20 100-m point count stations in each of the six study units. Each point count station was located 250 m apart and 250 m from the edge of the study unit and was visited three times approximately every two weeks between 22 May and 3 July. To ensure a consistent level of bird activity, we began point counts just after the dawn chorus and completed them within five hours. At each point, observers recorded all birds detected during a five-minute count period, and estimated the distance to each individual observed in distance classes 0–10 m, 10–25 m, 25–50 m, 50–75 m,

75–100 m, and >100 m (protocol *available online*).⁶ Point count surveys were conducted from 2002–2006 at all locations, resulting in a total of three years pre-burn and two years post-burn at one location, and two years pre-burn and three years post-burn at two locations. To create a balanced design we used two years pre-burn and two years post-burn at all locations.

Accurately estimating distances to an observation can be difficult (Johnson 2008); recent research has demonstrated that observers have more difficulty accurately estimating distances beyond 67 m (Alldredge et al. 2007). Therefore, we truncated the data for our analyses at 75 m to minimize incorrectly categorizing the further distance classes.

Model overview

Multispecies site occupancy models have been described previously by Dorazio and Royle (2005), and Dorazio et al. (2006), and applied in a number of different experimental survey situations (Kéry and Royle 2008a, b, Kéry et al. 2009). The basic sampling design is often referred to as the “robust design” (Pollock 1982). Under this design, sampling occurs in a number of “primary periods” (e.g., years) among which occupancy status of sites may change due to local extinction and colonization events. Secondary samples (e.g., daily visits) are obtained within each primary period, and over this shorter time frame, demographic closure is assumed. Closure in the context of modeling the dynamics of species occurrence implies that occupancy status is consistent at a point within a sampling season. For species with breeding seasons that only partially overlap the sampling period, this will lead to lower estimated detection rates than species which are present at the site for the entire sampling period.

To model occupancy dynamics across seasons, we allow for Markovian dependence in occupancy state (i.e., occupancy rate at time t is partially dependent on the occupancy state at time $t - 1$) as in the “multi-season” occupancy model (MacKenzie et al. 2002, Royle and Kéry 2007). However, we consider the multivariate version of that model, where each species in the sample is governed by a distinct model, having species-specific parameters (detection probability, treatment responses, and term estimating correlations in presence/absence through time) that are related (among species) via a hierarchical model.

The community-level model is formulated in terms of species-specific occurrence for each site/survey location (in our case a point count station). The model formally distinguishes between true occupancy state of a site, $z(i, j, t)$, and the observed occupancy state during any particular sample of that site, $x(i, j, k, t)$, which is a binary variable representing the detection or non-detection of species i at location j during year t and

visit k . In general, the $z(i, j, t)$ are not completely observed; $z(i, j, t) = 1$ if

$$\sum_{k=1}^{k=\text{visits}} x(i, j, k, t) > 0.$$

However, if

$$\sum_{k=1}^{k=\text{visits}} x(i, j, k, t) = 0$$

then the species is either present and undetected and $z(i, j, t) = 1$ or the species is truly absent and $z(i, j, t) = 0$ (Dorazio et al. 2006). The partially observed $z(i, j, t)$ are regarded as latent variables or random effects in the model. The observed presence-absence $x(i, j, k, t)$ can only be 1 if $z(i, j, t) = 1$, but can be 0 for either true absence or undetected presence. In particular, we suppose that, conditional on $z(i, j, t)$, $x(i, j, k, t)$ are Bernoulli random variables having parameter $p(i, j, k, t)$ for occupied sites, and 0 for unoccupied sites. This assumption is expressed as

$$x(i, j, k, t) \sim \text{Bernoulli}[p(i, j, k, t) \times z(i, j, t)].$$

Thus, when $z(i, j, t) = 0$ (i.e., true absence), then the observations are fixed zeros. Otherwise, sampling zeros are allowed with probability $1 - p(i, j, k, t)$ (Royle and Kéry 2007, Royle and Dorazio 2008:83–127).

Because the state variables $z(i, j, t)$ are only partially observed, we require a model describing the relationship among the variables across space, time and species. Uncertainty about each latent state can be assessed given this model and the observations. Here, we adopt an extension of the dynamic model described in Kéry and Royle (2008b) to allow for multiple species. For species i , we assume the following Markovian structure relating $z(i, j, t)$ to the previous state:

$$z(i, j, t) \sim \text{Bernoulli}(\psi_{i,j,t})$$

where

$$\text{logit}(\psi_{i,j,t}) = \beta_i + \rho_i \times z(i, j, t - 1) \quad \text{for } t > 1$$

and

$$\text{logit}(\psi_{i,j,t}) = \beta_i + \rho_i \times z_0(i, j) \quad \text{for } t = 1$$

where $z_0(i, j) \sim \text{Bernoulli}(\rho_{0i})$, $\rho_{0i} \sim \text{Uniform}(0,1)$ and β_i and ρ_i are normally distributed species-specific random effects such that $\beta_i \sim \mathcal{N}(\mu_\beta, \sigma_\beta^2)$ and $\rho_i \sim \mathcal{N}(\mu_\rho, \sigma_\rho^2)$, and ρ_i is a species-specific parameter that governs the “local survival” probability for species i . That is, local survival probability = $\Pr(z(i, j, t) = 1 \mid z(i, j, t - 1) = 1) = \beta_i + \rho_i$. Conversely, the local colonization probability for species i is $\Pr(z(i, j, t) = 1 \mid z(i, j, t - 1) = 0) = \beta_i$.

Modeling detection probability

Detection probability of species i at time t is $p_{i,t}$, where $\text{logit}(p_{i,t}) = \eta_i + \beta_t$, and η_i represents species-specific effects on detection and β_t represents year-specific

⁶ <http://www.rmrs.nau.edu/wildlife/birdsnburns/>

effects. We assumed $\eta_i \sim N(0, \sigma_p^2)$. For the basic model, detection probability is assumed to be species and year dependent. We included the year of survey to reflect potential differences in detection rates for different field crews, and potentially measure improvement in the crews' detection rates over the years of the study.

Treatment effects

Our analysis included two years of pre-burn and two years of post-burn data from each site. To evaluate the treatment effects on the avian community, we included the term: $\alpha \times \mathbf{TRT}(j, t)$ in the occurrence model so that $\text{logit}(\psi_{i,j,t}) = \beta_i + \rho_i \times z(i, j, t-1) + \alpha_i \times \mathbf{TRT}(j, t)$. $\mathbf{TRT}$ is a matrix of j sites by t times and consists of a 0 indicating the site has not been burned or a 1 indicating that the site has been burned and α_i is the species-specific effect of the treatment, which we assumed to be a random effect such that $\alpha_i \sim N(\mu_\alpha, \sigma_\alpha^2)$. We also included a term to allow for a treatment effect on detection probability so that

$$\text{logit}(p_{i,t}) = \eta_i + \beta_t \times \mathbf{TRT}(j, t)$$

where β_t is the effect of treatment on detection probability.

Inference

The statistical objective of the community-level model is to estimate the structural parameters including $(\mu_\beta, \sigma_\beta^2, \mu_p, \sigma_p^2)$ and to obtain estimates of certain functions of the latent state variables $z(i, j, t)$ that described changes in community structure or composition. To estimate these quantities, we performed a Bayesian analysis of the model in the freely available software package WinBUGS (Spiegelhalter et al. 2003). This hierarchical formulation of multi-species occupancy models is well-suited for implementation in WinBUGS because the constituent models for both occurrence and detection probability are simple binomial models. Additional motivation and discussion of this model can be found in Royle and Kéry (2007) and Kéry et al. (2009).

The WinBUGS model specification for the model described above is given in Supplement 1. We ran two parallel chains of length 35000 and discarded the first 5000 as burn-in and a thinning rate of 10. Convergence was assessed using the Gelman-Rubin diagnostic (Brooks and Gelman 1998).

Quantification of community-level changes

We estimated species richness for treatment plots and control plots separately, where species richness at time t is

$$N(t) = \sum_{i=1}^{i=\text{nspp}} \sum_{j=1}^{j=\text{sites}} z(i, j, t)$$

where nspp is the number of species.

We estimated species turnover (τ), the probability that a species selected at random from the community at time

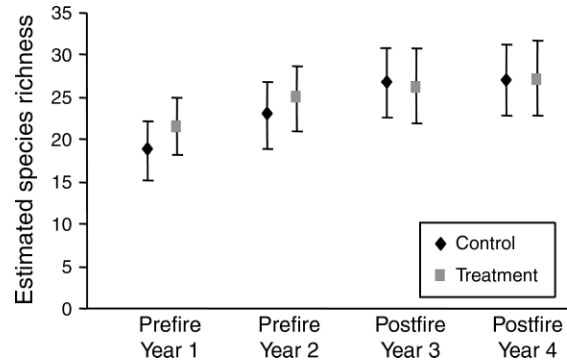


FIG. 1. Estimates of species richness at the point on three control and three treatment study units in the Okanogan-Wenatchee National Forest (Washington, USA) for two years prefire and two years postfire. Bars are 95% credible intervals.

t is a “new” species (not present at the community in time $t-1$) (Williams et al. 2002), and extinction rates (ϵ):

$$\tau(t) = \frac{\sum_{i=1}^{i=\text{nspp}} \sum_{j=1}^{j=\text{sites}} z(i, j, t) \times [1 - z(i, j, t-1)]}{\sum_{i=1}^{i=\text{nspp}} \sum_{j=1}^{j=\text{sites}} z(i, j, t-1)}$$

$$\epsilon(t) = \frac{\sum_{i=1}^{i=\text{nspp}} \sum_{j=1}^{j=\text{sites}} [1 - z(i, j, t)] \times z(i, j, t-1)}{\sum_{i=1}^{i=\text{nspp}} \sum_{j=1}^{j=\text{sites}} z(i, j, t-1)}$$

RESULTS

Basic model

Point count surveys detected 62 avian species during the study period (Appendix A). The most commonly detected species were Western Tanager, Red-breasted Nuthatch, Chipping Sparrow, Hammond's/Dusky Flycatcher, Yellow-rumped Warbler, Mountain Chickadee, and Dark-eyed Junco (Appendix A). There was a trend toward an increasing estimated number of species per point during the study period that was similar on both control and treatment locations for all years of the study (Fig. 1). Turnover and extinction rates were also similar on control and treatment locations before, during, and after prescribed fire treatments (Fig. 2). Estimates of species per point on control locations in pre-burn year 1 and post-burn year 2 did not overlap (95% CI pre-burn year 1 [15.25–22.08], 95% CI post-burn year 2 [22.83–31.23]), however estimates overlapped for treatment and control units in all years.

Treatment effects

Evidence for a statistically significant effect (i.e., 95% CI of parameter estimates of the treatment effect did not contain zero) of prescribed fire treatments on

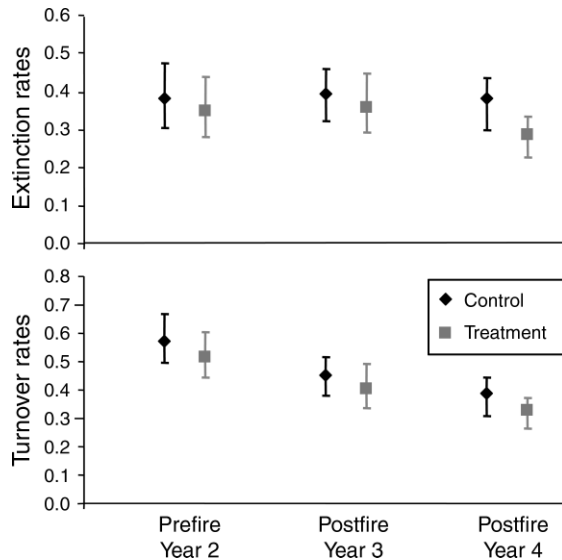


FIG. 2. Estimates of turnover and extinction rates on three control and three treatment study units in the Okanogan-Wenatchee National Forest, for prefire conditions (year 1 to year 2 of the study), prefire to postfire conditions (year 2 to year 3 of the study), and postfire conditions (year 3 to year 4 of the study). Turnover (τ), is the probability that a species selected at random from the community at time t is a "new" species. Extinction is the probability that a species that occupied a site in time t did not occupy the site in time $t + 1$. Bars are 95% credible intervals.

occupancy rates was observed for 12 avian species (Table 1, Fig. 3, Appendix B). We saw no significant effect of prescribed fire on overall detection probability of species (-0.017 , 95% CI $[-0.127-0.086]$). Seven species responded positively to prescribed fire, whereas five responded negatively (Fig. 4). Species responding positively included Black-backed and Hairy Woodpeckers, and White-breasted Nuthatches, all bark insectivore, cavity-nesting species. We did not detect evidence of a response by other cavity-nesting species such as Mountain Bluebirds, Lewis's or Three-toed Woodpeckers.

Three aerial insectivore species, Western Bluebird (which also forage on the ground), Western Wood-Pewee, Gray Flycatcher, and the open-ground insectivore American Robin, also responded positively to prescribed fire (Table 1, Figs. 3 and 4). We did not detect responses for several other aerial insectivores, including the Pacific-slope Flycatcher, the Dusky/Hammond's Flycatcher, and Townsend's Solitaire.

Three of the five species responding negatively to fire were foliage insectivores including Cassin's Vireo, Ruby-crowned Kinglet, and Swainson's Thrush. We failed to detect a response to fire for the foliage gleaning Mountain Chickadee, Golden-crowned Kinglet, Warbling Vireo or Western Tanager. Pine Siskin and Clark's Nutcracker, two seed specialists that also consume insects (Dawson 1997, Tomback 1998), declined after fire as well.

Species persistence

Estimates of ρ for all species (Fig. 5) were positive, indicating at least some degree of local persistence. The species with the highest values of ρ were Spotted Towhee 0.957 (95% CI $[0.882-0.987]$), Nashville Warbler 0.919 (95% CI $[0.979-0.996]$), and Warbling Vireo, 0.916 (95% CI $[0.979-0.996]$), indicating that these species were very likely to be observed at the same point count stations every year. Two common species, the Dark-eyed Junco ($\rho = 0.529$, 95% CI $[0.383-0.679]$) and the Pine Siskin ($\rho = 0.543$, 95% CI $[0.373-0.732]$) displayed the lowest estimated persistence.

DISCUSSION

Increasing interest in assessing the impacts of land management decisions on wildlife communities has lead to the implementation of large-scale field experiments designed to quantitatively assess population changes following habitat manipulations (Block et al. 2001, Converse et al. 2006). By extending the hierarchical Bayesian models of Dorazio et al. (2006), we present an approach to estimate the changes in occupancy rates, accounting for detection probability, for multiple species in response to environmental disturbances. The main advantage to this model for analyzing multispecies data sets, is that it provides a composite estimate of the response that applies to the community of observed species vs. a smaller subset of relatively common species chosen to satisfy what is usually a subjective sample size threshold. We devised a dynamic occupancy model that represents an extension of Kéry et al. (2009) to accommodate the multiyear structure of the data. The model is best described as a multispecies occupancy model for an open system. Whereas Kéry et al. (2009)

TABLE 1. List of 12 species for which we detected evidence of a response to prescribed fire treatments in the mixed-conifer forest of the Okanogan National Forest, Washington, USA.

Species	Forage guild	Nest layer	Nest type	Response
Hairy Woodpecker	BI	CA	C	pos
Black-backed Woodpecker	BI	CA	C	pos
Western Wood-Pewee	AI	CA	O	pos
Gray Flycatcher	AI	SH	O	pos
Cassin's Vireo	FI	CA	O	neg
Clark's Nutcracker	SS	CA	O	neg
White-breasted Nuthatch	BI	CA	C	pos
Ruby-crowned Kinglet	FI	CA	O	neg
Western Bluebird	AI	CA	C	pos
Swainson's Thrush	FI	SH	O	neg
American Robin	GI	CA	O	pos
Pine Siskin	SS	CA	O	neg

Notes: Foraging guilds are: BI, bark insectivore; AI, aerial insectivore; FI, foliage insectivore; SS, specialist seed forager. Nest layers are: CA, canopy to subcanopy; SH, shrub; GR, ground. Nest types are: O, open; C, closed (cavity-nesting species) (from Dawson [1997], Tomback [1998], and Saab and Powell [2005]). Responses are: pos, increased rates of occupancy in response to prescribed fire; neg, decreased occupancy rates in response to prescribed fire. See Appendix A for scientific names.

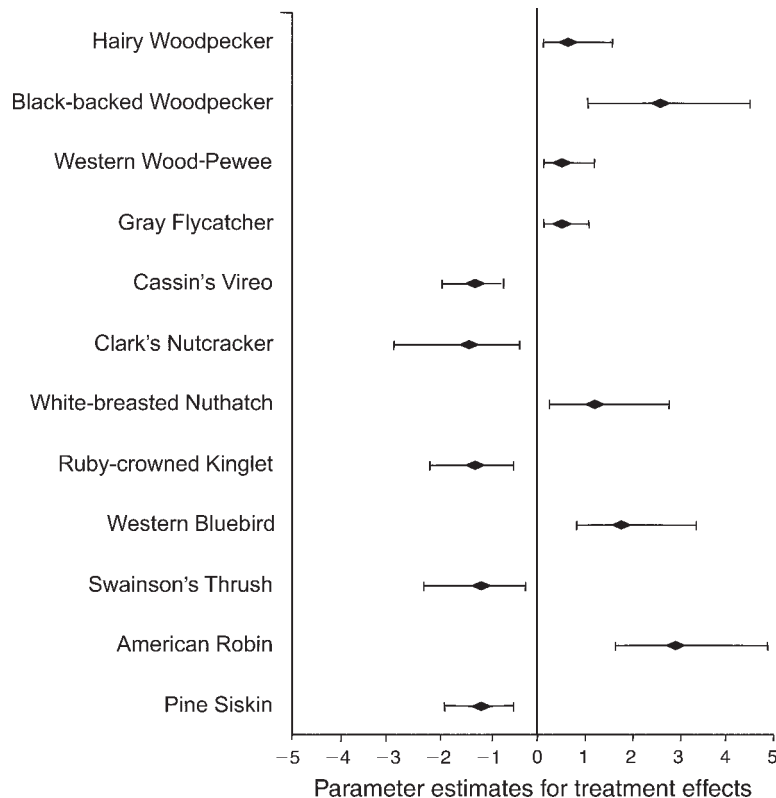


FIG. 3. Estimates of α (effect of prescribed fire) on occupancy rates for 12 species of songbird detected on six study units in the Okanogan-Wenatchee National Forest that responded to prescribed fire treatment (i.e., 95% credible intervals do not contain zero). Species with estimates below zero declined postfire, and species with estimates above zero increased postfire.

assumed random entry and exit from the population exposed to sampling, our model incorporates a Markov process that allows us to assess a given species occupancy status at time t dependent upon its occupancy state at the previous time step. Additionally, Kéry et al. (2009) accounted for the unobserved species complement that should normally be regarded as important in many analyses (Kéry and Schmidt 2006). We ignored that component of the model here and, instead, condition on the collection of observed species. As such, our model could be viewed as a “composite analysis” of all observed species, as opposed to a model of the “true” community. We did this for a practical reason: it would be difficult to convince a regulatory agency that an effect is real if it is primarily influenced by unseen, hypothetical species that did not show up in the sample. We believe that such hypothetical species represent an interesting statistical phenomenon and the biasing effect of sampling is a very real ecological concern, but the practical implications of basing management or conservation actions on these hypothetical species poses many important problems that are beyond the scope of this paper.

The main purpose of the multispecies model is to provide a composite assessment of community dynamics and the influence of habitat and other factors. While the model does improve inferences for all species (see

Appendix B) due to the group structure (random effects), it is not a panacea for sparse data. For example, uncertainty associated with the estimates of occupancy and treatment effects were large for species such as White-headed Woodpecker, (listed as species-of-concern by Partners in Flight, Audubon of Washington, and the Washington State Gap Analysis project), and Three-toed Woodpeckers, a species difficult to monitor due to their uncommon, local, and irruptive occurrences (Gunn and Hagan 2000). For these types of species, which are also of interest to land managers, concentrated single-species monitoring efforts may be required.

Our results evaluating prescribed fire effects generally concur with previous literature (cf. Saab and Powell 2005). Bark-gleaning individuals (with the exception of secondary cavity-nesting birds) and birds dependent on open-air maneuvers for foraging were more abundant after wildfire in Arizona, whereas foliage-gleaning insectivores were less common (Blake 1982). Smucker et al. (2005) observed increases in American Robin and Hairy Woodpecker after a moderate-severity wildfire in Montana, and decreases in Rudy-Crowned Kinglet, Swainson's Thrush, and Clark's Nutcracker, though population declines for the nutcracker were not statistically significant. Increases in American Robin, Hairy Woodpecker, and Western Bluebird after a wildfire were

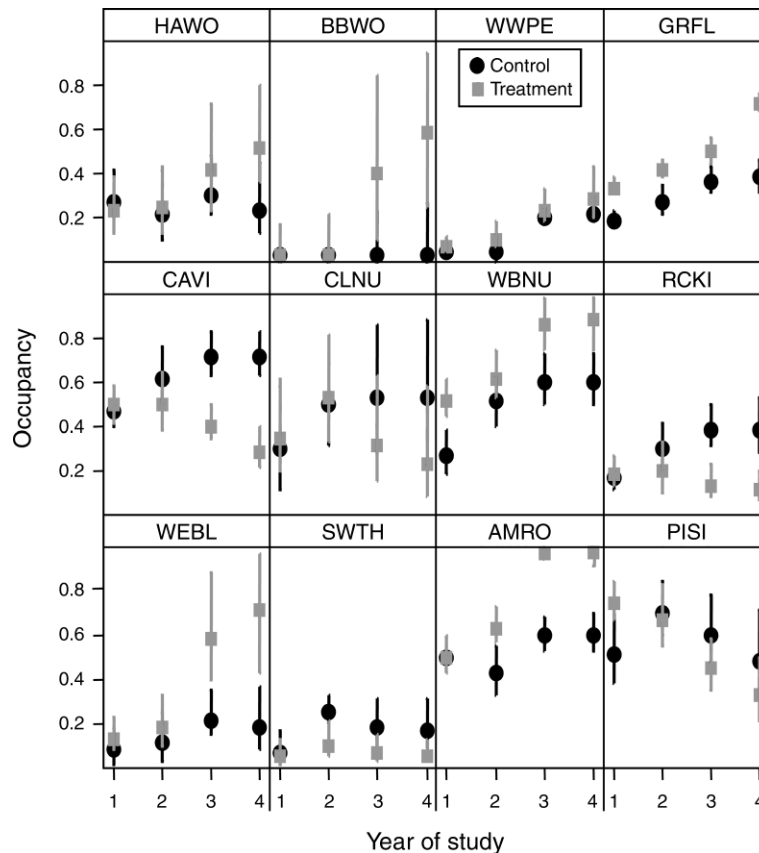


FIG. 4. Estimated Ψ (occupancy rate) for 12 avian species detected on six study units in the Okanogan-Wenatchee National Forest (three treatment and three control units) where evidence of a significant effect of prescribed fire on occupancy rate was observed (i.e., estimates of α did not contain zero) over years 1–4 of the study. Years 1 and 2 correspond to two years prior to prescribed fire, year 3 is the summer following the burn, and year 4 is two years after the burn. Error bars indicate 95% credible intervals. See Appendix A for species names.

also observed in the southwestern United States (Kotliar et al. 2007), and American Robin and White-breasted Nuthatch responded positively to prescribed fire in a ponderosa pine forest in California (George and Zack 2008).

Though we detected few changes in occupancy, other aspects of the avian community, such as nesting success, adult or juvenile survival rates, nest density, or abundance of a species may occur without associated changes in occupancy rates. For common species in our study densities changes may have occurred without accompanying changes in occupancy rates. Ecologists are well aware that abundance estimates can be misleading indicators of habitat quality (Van Horne 1983), however, evaluating multiple metrics such as nest success is a costly and time-consuming process, and generally, can only be feasibly accomplished for a few select species at a time.

Overall, we detected few statistically significant changes in the occupancy rates of members of the avian community, suggesting that fuels were reduced (Saab et al. 2006) without having large impacts on bird populations. Longer periods of posttreatment monitor-

ing may be necessary to detect responses by some bird species. For example, for cavity-nesting birds that appeared to benefit from prescribed fire, the long-term benefits are unclear. Low-intensity prescribed fires can create or destroy snags (Saab et al. 2006, Bagne et al. 2008), and few studies have followed the dynamics of snags or beetle populations following fire applications to determine the length of time beetle populations or standing snag numbers remain high after treatments, or how the delay in decay of newly created snags, which affects suitability for cavity excavation, affects populations of primary and secondary cavity-nesting birds and mammals.

Our findings that species richness was unaffected by prescribed fire treatments concurs with previous literature (George and Zack 2008, Hurteau et al. 2008). Researchers should carefully consider the scale at which inferences regarding community-level changes are made. Species richness is often used as a fundamental measure of community status (Dorazio et al. 2006). In some situations, alternative measures may be more useful, if for example, there are threatened or sensitive species in a community that is species poor. In our study, the

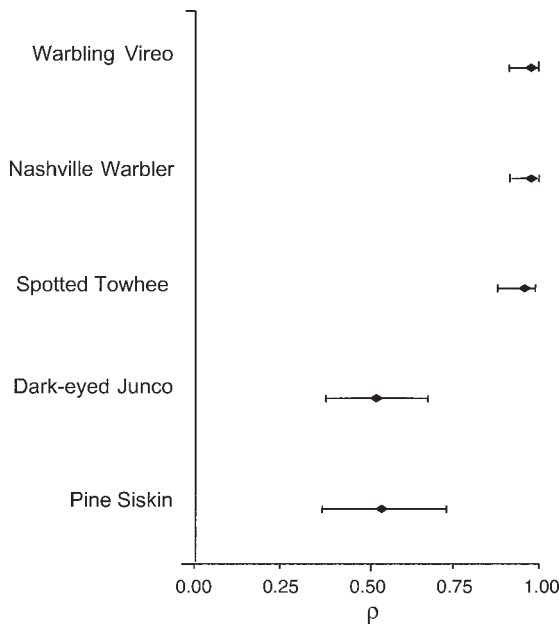


FIG. 5. Estimates of local survival probability, p , and 95% credible interval (correlation between occupancy at a point count station in one year with occupancy at the point count station in the previous year) for five species of songbird detected on six study units in the Okanogan-Wenatchee National Forest.

postfire community of bird species may contain the same number of species as the prefire community, but after the burn, the community may contain species that are not prevalent outside of burned areas, such as the Black-backed Woodpecker. Assessing both individual species responses to management practices and the overall contribution of a species to biodiversity on a larger regional scale (such as a forested area containing burned and unburned portions) is important for addressing specific management goals. Additionally, treatments on a study unit may affect dynamics on adjacent units by causing species to shift their distributions. For example, the increase in Clark's Nutcracker, Cassin's Vireo, and Ruby-Crowned Kinglet on control sites corresponding with the decline on treatment sites postfire may indicate short-term population shifts between study locations. Studies investigating how the large-scale dynamics of the wildlife community are affected by the size and spatial arrangement of treatment locations as well as the climatic conditions under which the treatments are implemented (i.e., wet or dry year) are needed. These studies, however, will require a monumental effort to implement.

Management implications

Ecological experiments are a vital step for understanding the mechanisms driving community structure despite the difficulty in obtaining large numbers of replicates. The BACI design provides a measure of protection against spurious results by controlling for pretreatment conditions, and adjusting estimates of population change

by measuring background temporal changes in populations on control plots (Block et al. 2001). Occupancy rates of several species of management interest including Hairy and Black-backed Woodpeckers increased after prescribed fire, indicating short-term positive effects on these species. Our results suggest that prescribed fire treatments in ponderosa pine forests of Washington had little or no short-term effect on the occupancy rates of many bird species. However, a lack of rapid responses to habitat changes after prescribed fire may be related to time lags created by site tenacity of breeding birds, suggesting that ecological field experiments require longer periods of posttreatment monitoring (Wiens and Rotenberry 1985). Longer-term data are also necessary to quantify the timeframe of negative impacts of prescribed fire on foliage gleaners, nutcrackers, and Pine Siskins. Fuel reduction treatments potentially reduce the risk of future severe wildfires and may be a practical management tool along the urban-wildland interface. Prescribed fire treatments, however, will likely not substitute for stand replacement fires in creating habitat for all fire-associated species. We recommend fire management plans that allow for natural wildfire events to burn in areas not likely to impact human developments or other areas of high economic or social value, thus, allowing for a mosaic of conditions that support diverse communities of avian species.

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APPENDIX A

List of species common names, scientific names, American Ornithologists’ Union codes, and total number of detections for a dry coniferous forest in Washington State, USA (*Ecological Archives* A019-048-A1).

APPENDIX B

Estimates of alpha (the treatment effect) with random effects (i.e., the borrowing of information from other species) and without random effects (*Ecological Archives* A019-048-A2).

SUPPLEMENT 1

Annotated WinBUGS source code containing the models described in this paper (*Ecological Archives* A019-048-S1).