The Journal of Wildlife Management 75(5):1051–1060; 2011; DOI: 10.1002/jwmg.128

Research Article

Short-Term Responses of Birds to Prescribed Fire in Fire-Suppressed Forests of California

KAREN E. BAGNE,[1,2] *Department of Biology, University of California, Riverside, CA 92521, USA, and USDA Forest Service, Sierra Nevada Research Center, 2081 E. Sierra Avenue, Fresno, CA 93710, USA*

KATHRYN L. PURCELL, *USDA Forest Service, Sierra Nevada Research Center, 2081 E. Sierra Avenue, Fresno, CA 93710, USA*

ABSTRACT Prescribed fire is one tool for restoring fire-suppressed forests, but application of fire during spring coincides with breeding and arrival of migrant birds. We examined effects of low-severity prescribed fires on counts of birds in a managed forest in the Sierra Nevada of California immediately, 1 year, and 3–6 years after fire was applied in spring. Of 26 species analyzed, counts of 3 species increased after fire (Pacific-slope flycatcher [*Empidonax difficilis*], brown creeper [*Certhia americana*], and American robin [*Turdus migratorius*]), and 6 species decreased after fire (Anna's hummingbird [*Calypte anna*], Hutton's vireo [*Vireo huttoni*], warbling vireo [*Vireo gilvus*], golden-crowned kinglet [*Regulus satrapa*], Nashville warbler [*Vermivora ruficapilla*], hermit warbler [*Dendroica occidentalis*]). Black-throated gray warbler (*Dendroica nigrescens*) increased in the first year following fire but decreased 3–6 years after fire. When grouped into guilds, habitat association and foraging guild best explained responses to fire, with the greatest changes occurring for oak-associated species (negative), riparian-associated species (positive), aerial foragers (positive), and bark foragers (positive). Lastly, when we compared our counts to those collected during the 1910s, changes were consistent with those predicted from fire suppression and species' affinity for burned forests, suggesting that results from contemporary fire studies should be interpreted within an ecological context that includes effects of fire suppression. We found that low-severity prescribed fires applied in spring served to drive the bird community towards pre-suppression conditions. © 2011 The Wildlife Society.[†]

KEY WORDS avian ecology, birds, fire suppression, forest, Joseph Grinnell, prescribed fire, Sierra Nevada.

Historically, much of the lower-elevation forest in the Sierra Nevada of California was characterized by large, widely spaced trees maintained by surface fires (Vankat and Major 1978, Minnich et al. 1995). Fire suppression was adopted as policy on federal and state lands in California by 1925, and consequently tree densities, occurrence of shade-tolerant species, accumulation of woody debris, fire intensities, and fire-return intervals increased (Vankat and Major 1978, Parsons and DeBenedetti 1979, Biswell 1989, Minnich et al. 1995). Prescribed fire is commonly used to reduce accumulation of fuels that result from fire suppression (Pollet and Omi 2002, Graham et al. 2004, Finney et al. 2005). Managers typically ignite prescribed fires when intensities will be low, such as in spring, presenting a potential conflict with breeding activities of forest birds (Erwin and Stasiak 1979, Kruse and Piehl 1986).

Land management decisions, such as implementation of prescribed burning, involve balancing targets with a wide variety of potential costs and benefits related to human and natural communities. Avian communities are a diverse and important component of natural communities, but responses of birds to prescribed fire are not well studied in Western forests (Finch et al. 1997, Kotliar et al. 2002, Saab and Powell 2005). Additionally, few studies have examined how birds respond to fires ignited in the spring (Kruse and Piehl 1986, Robel et al. 1998) when fires can destroy nests or nest sites and disrupt activities related to breeding, such as territory establishment. In general, however, prescribed fire reduces populations of ground and shrub nesting birds (Wilson et al. 1995, Artman et al. 2001, Blake 2005), while benefiting populations of woodpeckers (Granholm 1982, Blake 2005, Russell et al. 2009) and species that forage in the air and on the ground (Wilson et al. 1995, Artman et al. 2001, Blake 2005, Saab et al. 2007, Russell et al. 2009).

Our purpose was to explore how abundance of birds changed in response to prescribed fires set in the spring in the Sierra Nevada, California, where populations of many common avian species are declining (Siegel and DeSante 1999). Fires were set as part of a fuels reduction program in forests dominated by ponderosa pine (*Pinus ponderosa*) where fires had been suppressed for ≥50 years. We examined changes in counts of individual species and species guilds to identify more general habitat relationships that may be associated with responses to fire. We evaluated responses of birds to prescribed fire over 3 time periods: immediately or <2 months, 1 year, and 3–6 years after fire.

Received: 30 September 2008; Accepted: 15 October 2010; Published: 22 April 2011

[1]*E-mail: kbagne@gmail.com*

[2]*Present Address: USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM 87102.*

If active suppression of fires has altered current forest structure and composition as many studies have shown (Vankat and Major 1978, Parsons and DeBenedetti 1979, Biswell 1989, Minnich et al. 1995), we would expect these changes to have affected the bird community. Information on bird populations prior to fire suppression could provide perspective on the effects of suppression and the restorative potential of prescribed fires and other treatments. One of the earliest datasets that includes count data rather than just species presence data was collected during surveys headed by Joseph Grinnell from 1914 to 1920 in the Sierra Nevada (Grinnell and Storer 1924). Although impacts from Euro-American settlement were already present by this time, we assumed that bird communities were still largely influenced by natural fire regimes. We compared our data from fire-suppressed forests to this historical dataset to examine if elimination of fire has affected bird abundances and to evaluate the potential of prescribed fire to restore avian communities.

STUDY AREA

Our study area was in the Sierra Nevada within the Big Creek watershed tributary to Kings River between 1,000 m and 1,400 m elevation in the Sierra National Forest, Fresno County, California (37°02′ N, 119°15′ W). Forests were dominated by ponderosa pine mixed with canyon live oak (*Quercus chrysolepis*), California black oak (*Quercus kellogii*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*). Mountain misery (*Chamaebatia foliolosa*) was the dominant ground cover. Study sites included riparian elements, granitic outcrops, and shrub fields dominated by whiteleaf manzanita (*Arctostaphylos viscida*). Fires in the region had been regularly suppressed since the mid-1900s; historically, however, fires are thought to have been surface fires of mostly low severity every 2–12 years (Kilgore 1981, Drumm 1996) or of varying intensity, with average return intervals of large fires every 50 years (Brown et al. 1999, Minnich et al. 2000). The area was being managed with prescribed fire and mechanical treatments by the United States Forest Service to reduce accumulated fuels.

METHODS

We selected 9 sites, each ≥40 ha, in mature forest. Beginning in 1997, the United States Forest Service burned portions of the study area in patches that ranged in size from 95 to 550 ha. Prior to this time, no fires had been recorded in the area for ≥50 years. Three of our sites were burned in April 1997, February 1998, and May 1998, respectively, prior to initiation of our study in 2001; we designated these sites as 3–6 years post-fire (Fig. 1, P1–P3). The remaining 3 sites were burned between 4 April and 11 April 2002; we designated these sites as 1 year post-fire (Fig. 1, B1–B3). Three sites were unburned throughout the study period (Fig. 1, U1–U3). Fire crews set fires using drip torches and conditions at ignition were similar for all fires.

We measured changes to vegetation before and after burning in 2002 at 33 and 34 random points at 2 sites (Fig. 1, B2 and B3). We took measurements in an 11.3-m-radius circle (0.04 ha) centered on each random point, generally following methods described by Martin et al. (1997). Within each plot, we recorded all trees and snags ≥3 cm diameter at breast height by species and classified into 5 diameter at breast height categories (3–8 cm, 8.1–23 cm, 23.1–38 cm, 38.1–53 cm, >53 cm). We counted logs ≥8 cm in diameter and 1.0 m in length within a 5-m-radius circle, and we counted logs ≥23 cm in diameter and 1.0 m in length in the entire 11.3-m-radius circle. To obtain estimates of vegetative cover, we recorded plant species along 10-m transects extending from the plot center in the 4 cardinal directions. At 0.5-m increments along each transect, we recorded plant species intercepting a 2-m pole (James and Shugart 1970). We measured depth of forest litter at 1 m, 3 m, and 5 m from plot center for each transect. In addition to vegetation measurements, we also estimated the percentage of each 0.04-ha sampling plot that burned after prescribed fires.

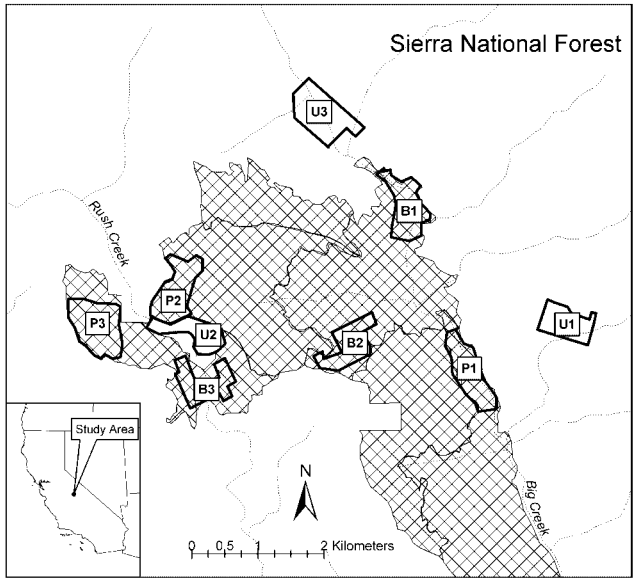

Figure 1. Map of sites we used to count birds from 2001 to 2003 in Sierra National Forest, California, USA. Unburned sites are designated by "U," sites burned in 2002 are designated by "B," and sites 3–6 years post-fire are designated by "P." Hatching indicates area where prescribed burns were being implemented by the United States Forest Service.

We estimated fire severity following prescribed fires for all 6 burned sites based on bole char heights where flames charred trunks of trees (U.S. Park Service 2003), and we averaged fire severity for 5 live trees near bird nests monitored as part of another study. Although fire severity may affect how birds select nests sites, nest-site selection should be similar among burned sites making our measure of fire severity comparable among sites.

We recorded data on numbers of breeding birds in 2001, 2002, and 2003 between 21 April and 23 May each year. We conducted surveys using a fixed-distance line transect method (Jarvinen and Vaisanen 1975, Verner 1985) on 6 visits to each site during the 4-week sampling period for a total of 162 counts. We permanently marked with posts a 1,000-m transect, consisting of a continuous line or multiple segments, every 50 m on each site. Parallel segments were

≥250 m apart. We surveyed each transect over a 1-hr period (3 min per 50-m segment) beginning at 0730 hours. Limitations to survey time and duration reduced potential temporal variation in detection rates. We recorded all birds seen or heard as either within or outside of a 50-m band on either side of the line. We did not conduct surveys in inclement weather conditions such as rain, snow, or wind.

The number of observers within a year varied from 3 to 6. Three observers surveyed sites in all 3 years, with 3 additional observers in 2001 and 1 additional observer in 2002, for a total of 7 different observers during the 3 years of the study. We trained all observers on methods with local birds for ≥2 weeks prior to surveys and observers passed standard hearing tests. All observers visited all sites within a year to help control for observer bias.

To allow inferences that included more species and to facilitate comparisons with previous studies, we examined nesting guilds, foraging guilds, habitat associations, and migratory status based in part on information in Granholm (1982) and Beedy and Granholm (1985; Appendix). We summed counts over species within guilds for species with total counts >10 over 3 years.

Historical Perspective

To examine how bird communities have changed over time, we compared data from our study to a historical dataset collected by Grinnell and Storer (1924) in Yosemite National Park, approximately 80 km north of the study area. Grinnell's and Storer's (1924) surveys included the number of each species detected, approximate path of the observer, and total time spent recording. Locations surveyed within Yosemite Valley most closely matched ours in elevation and dominant tree species, although plant communities differed to some extent. We selected only morning surveys between mid-April and mid-May (29 Apr 1916, 15 May 1919, and 16 May 1919). We created a matching dataset of 3 contemporary 1-hr counts by averaging sets of 10 counts from unburned sites that occurred within 2 days of each date of the historical counts. Because of the limited nature of the historical data, we examined differences qualitatively based on the average count per hour from the 2 time periods.

We wanted to assess whether changes in numbers of birds counted were consistent with predictions related to adoption of fire suppression policies, which occurred near the time of the historical counts. Specifically, if numbers of birds have been affected by fire suppression, we predicted that species that respond positively to fire would have declined and species that respond negatively to fire would have increased. To categorize species by their likely response to fire, we compiled responses published in the literature and avoided studies that included mechanical treatments except in 1 case where the vegetation treatment included fire, was designed to mimic historical conditions, and included several species of interest for which there were no other published results (Kilgore 1971). We included only those studies that examined low severity fires, which we felt would also be similar to prescribed fire and common historical fires. We did not attempt to reinterpret published data and simply compiled responses as noted by authors. We were particularly interested in the direction of response, but studies varied widely in scope and methods. Neutral responses likely included Type I errors, so we emphasized an identified response over non-response to categorize species by excluding results for species with <10 total detections and classifying a species as responding if ≥25% of published studies identified the species as responding positively or negatively to fire; we categorized all others as non-responding.

Statistical Analyses

We evaluated changes in vegetation by comparing measures before and after prescribed burning using a 2-sample *t*-test with a Satterthwaite adjustment for unequal variances. We assessed vegetation at 3 structural levels: ground, shrub, and tree. For ground level, we analyzed depth of litter (mm), numbers of small and large logs, and percent cover of mountain misery. For shrub level, we analyzed percent cover of all shrub species combined. For tree level, we analyzed the number of trees in each diameter class, with the 2 largest classes combined due to low numbers of large trees, and total number of snags ≥3 cm in diameter.

Our index of abundance was the mean number of individuals of a species counted over the 6 visits within a given year on each transect. Although we counted birds within and beyond a 50-m belt, we used all birds detected in our analyses because there was variation among observers in estimating the boundaries of the belt. Differences in rates of detection between burned and unburned areas are of concern (Buckland et al. 2001, Johnson 2007), although they may be limited with prescribed fire in these forest types (Russell et al. 2009). Most detections were aural and differences in sound attenuation between burned and unburned areas were unlikely to be large enough to affect counts considering that there were only minor changes to vegetation structure from patchy surface fires.

We evaluated changes in birds counted on burned transects relative to unburned for species with counts ≥35 per treatment (unburned, burned 2002, burned 1997–1998). For guilds, we summed the index across member species and burn effects analyzed similarly. We used generalized estimating equations (GEE) to fit generalized linear models with repeated measures, which we included to account for counting birds on the same site in multiple years. Because our data are a time series, we specified the covariance matrix as autoregressive (lag of 1 year), except in 1 case where the model did not converge and we used an exchangeable covariance matrix. We used a negative binomial distribution with a ln link function to model counts unless models would not converge or standard errors for the GEE estimates seemed unusually high, when instead we used a Poisson distribution. Standard errors remained high for the immediate and 1-year post-fire analyses of Hammond's flycatcher (*Empidonax hammondii*), thus we made no conclusions about response to fire within 1 year of burning for this species.

We used linear contrasts within GEE to examine differences in counts for 3 time periods post-fire (immediate, 1 year, and 3–6 years). For sites burned in 2002, we had

pre-burn data, thus we were able to evaluate responses to burning within a before–after control–impact (BACI) framework by examining the interaction of treatment (burned vs. unburned) and time (before vs. after; Underwood 1993). We evaluated 2 time periods in this analysis, the period immediately following ignition with counts completed within 2 months of burning (i.e., 2002 where fire was applied ≤2 weeks before counting) and 1 year after fire using counts from both 2002 and 2003. For the third time period (3–6 years post-fire), we lacked pre-burn data, therefore we assumed sites were similar prior to burning in 1997–1998. These models included survey year as well as treatment, the effect of interest. To aid interpretation, we back-transformed parameter estimates and standard errors to their original scale using e^x. We interpreted these estimates similar to regression coefficients with no effect equal to 1.0 (Hosmer and Lemeshow 2000).

RESULTS

Fires often burned for several weeks and were patchy in distribution, leaving unburned patches around rock outcrops and streams, creating a mosaic across sites. The area burned averaged 47% (SD = 39.6), with average bole char heights from 1997 to 1998 burns ($\bar{x}$ = 1.23 m, SD = 1.04, max. = 5 m) 43% higher than for 2002 burns ($\bar{x}$ = 0.86 m, SD = 0.92, max. = 4.4 m). Litter depth and shrub cover were reduced after fire and cover of mountain misery increased; numbers of logs, trees, and snags in all size classes did not change (Table 1).

We analyzed counts of 26 individual species (Table 2). Overall, counts of 6 species decreased and 3 species increased at some point after fire (Table 2). Counts of Anna's hummingbird (*Calypte anna*) were reduced 65% immediately following burning, and Hutton's vireo (*Vireo huttoni*), golden-crowned kinglet (*Regulus satrapa*), and hermit warbler (*Dendroica occidentalis*) were reduced throughout the first year after fire. Counts of Nashville warbler (*Vermivora ruficapilla*) and warbling vireo (*Vireo gilvus*) were lower 3–6 years after fire by 61% and 59%, respectively. Counts of American robin (*Turdus migratorius*) increased after fire during all 3 time periods, Pacific-slope flycatcher (*Empidonax difficilis*) only increased within 1 year of fire, and brown creeper (*Certhia americana*) only increased during the period 3–6 years after fire. Black-throated gray warbler (*Dendroica nigrescens*) was the only species with a mixed response; counts increased approximately 24% within 1 year of burning but decreased by 75% 3–6 years post-fire (Table 2). Changes in all species combined as well as mountain quail (*Oreortyx pictus*), Cassin's vireo (*Vireo cassinii*), and spotted towhee (*Pipilo maculatus*) were <10% across all time periods.

For species' guilds, counts of riparian-associated species and aerial foragers increased within 1 year of fire, whereas counts of bark foragers increased only 3–6 years after fire (Table 3; Appendix). In contrast, counts of conifer-associated species decreased by 18% within 1 year of fire and counts of oak-associated species decreased 54% only 3–6 years after fire. Counts of canopy foragers decreased 18–27% within 1 year of fire, whereas understory foragers were consistently unaffected. Snag nesters were the only nesting guild that responded to fire and were 76% more abundant on sites 3–6 years after fire (Table 3).

Historical Perspective

Although the overall rate of detections was similar between historical and contemporary counts ($\bar{x}$ = 95.3/hr, SD = 14.7 vs. 98.4/hr, SD = 4.8, respectively), the distribution of counts differed by species (Table 4). Presence of brown-headed cowbirds (*Molothrus ater*) in contemporary counts is conspicuous.

We compiled observed responses of bird species to fire from 13 published studies and this study (Table 4). We could find no published results that met our criteria for 4 species and, thus, used responses from our current analysis exclusively (Table 4). We expected positive responders to low severity fire to have declined in the absence of fire, which was true for 4 of 7 species (black-headed grosbeak [*Pheucticus melanocephalus*], American robin, western wood-pewee [*Contopus sordidulus*], and yellow-rumped warbler [*Dendroica coronata*]; Table 4). We expected negative responders to increase in the

Table 1. Vegetation variables measured before (1996–1999) and after (2002) burning on random 0.04-ha plots (n = 67) in Sierra National Forest, California, USA. We measured diameter at breast height at 1.3 m from the ground. Mountain misery (*Chamaebatia foliolosa*) was the dominant ground cover species.

	Before		After			
Vegetation variable	$\bar{x}$	**SE**	$\bar{x}$	**SE**	***t***	***P***
Ground level						
Litter depth (mm)	73.8	4.6	15.9	1.3	−12.06	<0.001
No. of logs >23 cm diam	4.2	0.5	4.1	0.5	−0.07	0.95
No. of logs 8–23 cm diam[a]	4.0	0.5	4.0	0.5	−0.15	0.88
Percent cover mountain misery	21.3	3.7	30.7	2.8	2.02	0.045
Shrubs						
Percent shrub cover	13.4	2.3	5.6	1.0	−3.13	0.002
Trees						
No. of live trees 3–8 cm dbh	44.8	4.2	44.4	4.2	−0.06	0.95
No. of live trees 8.1–23 cm dbh	25.6	3.0	28.4	2.9	0.68	0.49
No. of live trees 23.1–38 cm dbh	5.0	0.5	5.3	0.5	0.41	0.68
No. of live trees >38 cm dbh	3.3	0.3	3.6	0.3	0.65	0.52
No. of snags ≥3 cm dbh	17.0	3.2	25.7	3.4	1.87	0.06

[a] Measured in a 5-m radius circle and thus is per 0.008 ha.

Table 2. Results from negative binomial or Poisson regression analysis of fire effects on counts of individual bird species for 3 time periods encompassing bird counts from 2001 to 2003 and fires set 1997–2002 in Sierra National Forest, California, USA. We based estimates (e^x where x = parameter estimate from ln link model) of fire effects from generalized estimating equations (GEE) models on contrasts for each time period. Estimates of immediate (<2 months post-fire) and 1 year post-fire are from the interaction of time × treatment in a before–after control–impact (BACI) context. Estimates for sites 3–6 years post-fire contrast burned and unburned sites but do not include prefire data.

	Immediate[b]			1 year post-fire[c]			3–6 years post-fire vs. unburned[c]		
Species[a]	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Mountain quail	0.93	0.32	0.83	1.03	0.28	0.90	0.95	0.15	0.75
Anna's hummingbird	0.35	0.20	0.03	0.57	0.38	0.31	1.09	0.28	0.73
Acorn woodpecker	0.94	0.23	0.79	0.92	0.27	0.77	0.66	0.26	0.24
Northern flicker	0.80	0.13	0.16	0.81	0.13	0.17	1.17	0.15	0.23
Western wood-pewee	1.00	0.20	1.00	1.12	0.25	0.59	0.79	0.55	0.68
Hammond's flycatcher	3.75	5.30[d]	0.14	3.70	4.90[d]	0.13	0.62	0.45	0.41
Pacific-slope flycatcher	1.86	0.41	0.004	1.86	0.43	0.005	1.10	0.65	0.86
Cassin's vireo	1.01	0.19	0.95	1.01	0.18	0.94	1.00	0.28	1.00
Hutton's vireo	0.60	0.15	0.04	0.62	0.13	0.02	0.68	0.18	0.12
Warbling vireo	1.08	0.20	0.67	1.18	0.17	0.26	0.41	0.21	0.046
Steller's jay	0.89	0.13	0.42	0.95	0.20	0.79	1.01	0.14	0.96
Red-breasted nuthatch	0.94	0.31	0.83	0.96	0.30	0.89	1.78	0.78	0.15
Brown creeper	1.62	0.47	0.08	1.30	0.25	0.16	2.36	0.90	0.02
Winter wren	0.80	0.18	0.32	0.83	0.15	0.27	1.13	0.97	0.85
Golden-crowned kinglet	0.13	0.06	<0.001	0.21	0.08	<0.001	1.04	0.73	0.94
American robin	2.25	0.65	0.003	2.07	0.71	0.02	1.58	0.35	0.03
Nashville warbler	0.73	0.15	0.11	0.74	0.16	0.14	0.39	0.15	0.008
Yellow-rumped warbler	1.20	0.49	0.62	1.23	0.40	0.50	1.47	0.34	0.09
Black-throated gray warbler	1.24	0.11	0.02	1.24	0.13	0.046	0.25	0.11	<0.001
Hermit warbler	0.52	0.11	0.002	0.53	0.09	<0.001	0.74	0.29	0.40
Western tanager	0.57	0.22	0.12	0.68	0.28	0.30	0.96	0.31	0.89
Spotted towhee	0.93	0.12	0.58	0.92	0.12	0.51	1.06	0.20	0.74
Dark-eyed junco	0.86	0.23	0.54	0.87	0.22	0.58	1.30	0.21	0.11
Black-headed grosbeak	1.02	0.18	0.90	1.02	0.19	0.91	0.69	0.33	0.38
Brown-headed cowbird	0.76	0.23	0.34	0.71	0.15	0.11	1.01	0.38	0.98
Purple finch	1.36	0.47	0.34	1.06	0.31	0.82	1.03	0.28	0.91
Total abundance (all species)	0.92	0.07	0.33	0.96	0.08	0.99	0.99	0.04	0.76

[a] Scientific names are listed in Appendix.
[b] Counts from 6 sites and 2 years.
[c] Counts from 6 sites and 3 years.
[d] Due to high SEs, we considered these effects to be inconclusive because of poor model fit.

absence of fire, which was true for 7 of 9 species (Nashville warbler, spotted towhee, golden-crowned kinglet, Hutton's vireo, mountain quail, Hammond's flycatcher, Anna's hummingbird; Table 4). Changes in counts of Pacific-slope flycatcher and warbling vireo over time were opposite those predicted by our fire suppression hypothesis.

DISCUSSION

We observed short-term (≤6 yr) changes in relative abundance for 9 of 26 species in response to low severity prescribed fires (Table 2). Our findings and those from similar studies were consistent with respect to the direction of change for most species (Table 4).

Any aversion to smoke and flames during burning, which we thought would be especially probable in the spring, was either too weak or short-lived to detect, as nearly all species that responded immediately to fires showed a continued response 1 year after fire (Table 2). Therefore, aversion or attraction to burned areas seemed related to changes in vegetation or other resources that lasted into the following year. Although it appeared that breeding activities, such as singing, were not disrupted, nests are still vulnerable to fire in the spring (Kruse and Piehl 1986, Bagne and Purcell 2009).

Overall, counts of most species did not change in response to low severity spring fires. Heterogeneity in burning and restriction of fires to the understory may have left critical resources intact (Emlen 1970). The 2 low-nesting species that increased in response to fire, American robin and Pacific-slope flycatcher, nest in more mesic conditions (Small 1994) that are less prone to burning than the drier oak and shrub vegetation communities preferred by 2 low-nesting species that decreased in response to fire, black-throated gray warbler and Hutton's vireo (Small 1994). In contrast, strong stability in numbers, where there was <10% variation between counts in burned and unburned forests in any time period, included 2 ground nesting species and would seem to be due to more than just use of residual unburned patches. Behavioral plasticity and site fidelity have been suggested as mechanisms behind lack of response to disturbance (Wiens and Rotenberry 1985, Petersen and Best 1987) and likely played a role in our study.

Some guilds were useful in predicting responses to fire, particularly those related to foraging or habitat association. Both snag nesters and bark foragers, guilds with substantial overlap, increased in response to fire. Although snags are combustible, they are also created by fire (Bagne et al. 2008).

Table 3. Results from negative binomial or Poisson regression analysis of fire effects on guilds for 3 time periods encompassing bird counts from 2001 to 2003 and fires set 1997–2002 in the Sierra National Forest, California, USA. We based estimates (e^x where x = parameter estimate from ln link model) of fire effects from generalized estimating equations (GEE) models on contrasts for each time period. Estimates >1 indicate increases in response to prescribed fire and estimates <1 indicate decreases. Estimates of immediate (<2 months post-fire) and 1 year post-fire are from the interaction of time × treatment within a before–after control–impact (BACI) context. Sites 3–6 years post-fire contrast burned and unburned sites, but do not include prefire data.

	Immediate[b]			1 year post-fire[c]			3–6 years post-fire vs. unburned[c]		
Guild[a]	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Nesting guild									
Snag nesters	1.10	0.15	0.50	1.10	0.16	0.51	1.76	0.55	0.05
Ground nesters	0.83	0.12	0.19	0.85	0.13	0.29	0.89	0.08	0.22
High nesters	0.82	0.12	0.17	0.85	0.11	0.18	0.94	0.19	0.76
Low nesters	1.01	0.11	0.93	1.01	0.11	0.93	0.87	0.12	0.34
Migratory status									
Residents	0.87	0.11	0.24	0.87	0.10	0.23	1.16	0.12	0.14
Short-distance migrants	1.02	0.13	0.89	1.02	0.12	0.86	1.20	0.19	0.24
Long-distance migrants	0.95	0.08	0.51	0.96	0.10	0.57	0.76	0.08	0.006
Habitat association									
Oak associated	0.81	0.11	0.12	0.82	0.12	0.10	0.46	0.13	0.003
Riparian associated	1.57	0.19	<0.001	1.57	0.19	<0.001	1.21	0.38	0.53
Conifer associated	0.81	0.02	<0.001	0.82	0.01	<0.001	1.17	0.25	0.46
Open associated	0.90	0.12	0.40	0.90	0.15	0.52	1.17	0.10	0.07
Foraging guild									
Aerial foraging	1.71	0.42	0.03	1.71	0.43	0.03	1.15	0.233	0.62
Bark foraging	1.20	0.26	0.39	1.20	0.24	0.36	2.15	0.77	0.02
Understory foraging	0.96	0.07	0.58	0.96	0.08	0.60	1.09	0.08	0.25
Canopy foraging	0.81	0.09	0.06	0.82	0.10	0.09	0.73	0.08	0.006

[a] Guild assignments of species are listed in Appendix.
[b] Counts from 6 sites and 2 years.
[c] Counts from 6 sites and 3 years.

Counts of aerial foragers increased after fire, a result found in studies of both wildfire (Bock and Lynch 1970, Raphael et al. 1987, Kotliar et al. 2002, Morissette et al. 2002) and prescribed fire (Woinarski 1990, Artman et al. 2001). Counts of species associated with open forests, however, did not change nor were tree densities reduced. Aerial foragers may have responded to an increase in aerial insect prey (Granholm 1982). Unexpectedly, we found a decrease in counts of canopy foragers and high-nesting species despite minimal burning in the upper canopy. Although Granholm (1982) found a similar response to prescribed fire in foliage-gleaning insectivores suggesting that smoke and heat from the fire caused mortality of foliage insects, this does not explain the continued response we found for this group 3–6 years after fire.

We found changes in counts of 2 guilds that are conservation priorities in the Sierra Nevada: riparian and oak-associated species (Siegel and DeSante 1999). Riparian species increased in the first year following fire even though riparian areas seldom burned. Numbers of birds associated with oaks were lower with burning, although the fires did not reduce numbers of trees, including oaks. Oaks are uncommon compared to conifers in these forests but are disproportionately important for foraging and nesting (Rodewald 2003, Purcell and Drynan 2008). Regional declines of oak-associated species are thought to be due, in part, to poor oak regeneration that in mixed forests, such as those in our study, may be impeded by fire-suppression (McClaran and Bartolome 1989, Siegel and DeSante 1999, Garrison et al. 2002).

Vegetation measurements revealed a high density of trees on our contemporary unburned reference sites, which are characteristic of fire-suppressed forests in the region (Vankat and Major 1978, Parsons and DeBenedetti 1979, Minnich et al. 1995). We counted approximately 848 stems/ha >8 cm diameter at breast height (Table 1). The best historical dataset for stem density is from the 1930s in the San Bernardino Mountains, a more southerly range in California, with an average of 250 stems/ha >12 cm diameter at breast height (Minnich et al. 1995). Although repeated burning is planned for the study area, this first application of fire did little to restore past forest structure.

Although the forests we studied were altered to some extent by the time the historical data were collected (Gibbens and Heady 1964), changes in detection between the 1910s and the early 2000s corresponded with our predictions for most species, suggesting that suppression of fire in this fire-adapted landscape has likely altered structure of the bird community. Historical conditions and restoration goals are especially meaningful when they encompass evolutionary relationships such as the role natural fire regimes play in shaping bird communities (Hutto 2008). Significantly, early advocates of fire suppression failed to recognize these relationships (Greeley 1920, U.S. Biological Survey 1922).

MANAGEMENT IMPLICATIONS

The structure of natural communities surely reflects the consequences of important historical or cumulative impacts, such as fire suppression, which is significant for management and restoration. For example, species that decline in response to fire may not require special attention when planning burns if their populations are high as a result of fire suppression

Table 4. Average count/hr and SE of bird species surveyed 1916–1919 in Yosemite National Park, California, USA (Grinnell; $n = 3$) and 2001–2003 in Sierra National Forest, California, USA (unburned sites only; $n = 30$) grouped by predicted change in counts resulting from fire suppression. We predicted that species observed to have a positive response to low severity fire would decrease in response to fire suppression and have relatively high historical counts, whereas species observed to have a negative response to fire would increase and have relatively low historical counts. We compiled observed responses of bird species to fire from our study and other published studies based on the number of citations where ≥25% of authors observed a positive or negative response. We ordered species by response (positive, negative, none) and by descending magnitude of predicted change between mean counts. We ordered species with no observed response by descending difference between 2001–2003 counts and 1916–1919 counts.

	Observed response to fire			Predicted response	Count/hr			
Species	Positive	None	Negative	to fire suppression	1916–1919	SE	2001–2003	SE
Western wood-pewee	4[b,k,l,m]	3[a,c,g]	1[n]	Decrease	6.0	3.7	2.1	1.6
American robin	6[a,b,e,i,j,m]	6[c,d,f,g,l,k]		Decrease	5.6	1.1	2.2	0.4
Black-headed grosbeak	1[e]	3[a,b,c]		Decrease	9.7	4.9	6.4	0.5
Yellow-rumped warbler	2[c,g]	6[a,b,f,k,m,n]		Decrease	4.6	0.9	1.8	0.6
Western tanager	3[f,g,n]	5[a,b,e,l,m]		Decrease	3.3	2.5	3.6	1.1
Steller's jay	3[e,l,m]	4[a,b,c,m]		Decrease	2.6	1.1	3.4	0.8
Pacific-slope flycatcher	1[a]			Decrease	0		2.8	0.6
Nashville warbler		1[m]	2[a,b]	Increase	1.3	1.1	10.0	1.7
Spotted towhee	1[e]	2[a,m]	2[b,c]	Increase	1.9	1.4	9.4	2.4
Golden-crowned kinglet		1[m]	3[a,f,l]	Increase	0.3	0.4	3.9	1.5
Hutton's vireo			1[a]	Increase	0		3.4	0.9
Mountain quail		1[a]	1[b]	Increase	0.1	0.1	2.7	0.7
Hammond's flycatcher		3[a,b,f]	1[l]	Increase	0		1.8	0.3
Anna's hummingbird			1[a]	Increase	0		0.9	0.1
Hermit warbler		1[b]	1[a]	Increase	6.3	1.6	5.5	0.8
Warbling vireo		4[b,c,f,m]	2[a,k]	Increase	10.1	1.2	2.4	0.4
Dark-eyed junco	2[d,g]	9[a,b,f,h,i,k,l,m,n]		None	2.7	2.7	8.5	0.8
Black-throated gray warbler		1[a]		None	0.3	0.4	2.4	0.4
Winter wren		3[a,b,f]		None	0		1.9	0.5
Brown-headed cowbird	1[d]	7[a,f,g,h,i,k,m]		None	0		1.6	0.2
Acorn woodpecker		2[a,c]		None	0.3	0.4	1.7	0.4
Brown creeper	1[a]	5[b,f,g,l,m]		None	1.0	0.7	1.5	0.3
Northern flicker	1[d]	10[a,b,e,f,g,h,i,j,k,m]	1[l]	None	1.1	0.1	1.3	0.5
Red-breasted nuthatch	1[g]	5[a,b,f,l,m]	1[c]	None	2.6	1.1	2.4	0.8
Purple finch		2[a,b]		None	3.7	2.0	2.7	0.7
Cassin's vireo	1[g]	3[a,b,f]	1[m]	None	5.1	2.0	3.2	1.0

[a] Current study.
[b] Kilgore (1971).
[c] Kirkpatrick et al. (2006).
[d] White et al. (1999).
[e] Kotliar et al. (2007).
[f] Smucker (2005).
[g] Bock and Bock (1983).
[h] Wilson et al. (1995).
[i] Blake (2005).
[j] Artman et al. (2001).
[k] Dieni and Anderson (1999).
[l] Granholm (1982).
[m] Russell et al. (2009).
[n] Dickson et al. (2009).

(Beedy 1982), which was likely true for Hutton's vireo, golden-crowned kinglet, and Nashville warbler. This broader perspective can also be important for management of bird habitats. For example, prescribed fire appeared to be detrimental to oak-associated bird species because of short-term declines in burned areas. Because oaks depend on fire and other types of disturbances to regenerate, fire suppression will not maintain oak-associated bird species over the long term (Garrison et al. 2002). Ultimately, fire suppression will not benefit those species that respond negatively to fire, because fires cannot be suppressed indefinitely (Reinhardt et al. 2008). For species that responded positively to fire, such as riparian-associated species, prescribed fire could help reverse declining trends (Siegel and DeSante 1999). Because many of the changes we detected were in the direction that could shift bird numbers towards historical pattern of abundance, low severity prescribed fires have potential as a tool for restoring the structure of avian communities in forests where fires have been suppressed.

ACKNOWLEDGMENTS

Our study was funded, in part, by the Joint Fire Sciences Program (Project 00-2-05) and additionally by the U.S. Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center. We thank D. McCandliss, S. Parr, C. Ballard, and M. Helm of the Sierra National Forest for coordination and execution of prescribed burns. We also thank S. Sutton-Mazzocco, J. Hartwig, L. Nason, S. Deal, and particularly K. Mazzocco and D. Drynan for field

assistance. S. Mori and R. King provided assistance on statistical issues and SAS (SAS Institute, Cary, NC) code. R. Steidl, J. Rotenberry, R. Minnich, M. Allen, and anonymous reviewers provided input that improved the manuscript. C. Moritz and K. Klitz at the Museum of Vertebrate Zoology at University of California Berkeley kindly provided access to Grinnell's field notes.

LITERATURE CITED

Artman, V. L., E. K. Sutherland, and J. F. Downhower. 2001. Prescribed burning to restore mixed-oak communities in Southern Ohio: effects on breeding-bird populations. Conservation Biology 15:1423–1434.

Bagne, K. E., and K. Purcell. 2009. Lessons learned from prescribed fire in ponderosa pine forests of the southern Sierra Nevada. Pages 679–690 *in* T. D. Rich, C. Arizmendi, D. Demarest, and C. Thompson, editors. Tundra to tropics: connecting birds, habitats and people. Proceedings of the 4th International Partners in Flight Conference, 13–16 February 2008. McAllen, Texas, USA. Partners in Flight.

Bagne, K. E., K. L. Purcell, and J. T. Rotenberry. 2008. Prescribed fire, snag population dynamics, and avian nest site selection. Forest Ecology and Management 255:99–105.

Beedy, E. C. 1982. Bird community structure in coniferous forests of Yosemite National Park, California. Dissertation, University of California, Davis, USA.

Beedy, E. C., and S. L. Granholm. 1985. Discovering Sierra birds: western slope. Yosemite Natural History Association and Sequoia Natural History Association, Yosemite National Park, California, USA.

Biswell, H. H. 1989. Prescribed burning in Californian wildlands vegetation management. University of California Press, Berkeley, California, USA.

Blake, J. G. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. Biological Conservation 121:519–531.

Bock, C. E., and J. H. Bock. 1983. Responses of birds and deer mice to prescribed burning in ponderosa pine. Journal of Wildlife Management 47:836–840.

Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 14:513–532.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Dickson, B. G., B. R. Noon, C. H. Flather, S. Jentsch, and W. M. Block. 2009. Quantifying the multi-scale response of avifauna to prescribed fire experiments in the southwest United States. Ecological Applications 19:608–621.

Dieni, J. S., and S. H. Anderson. 1999. Effects of recent burning on breeding bird community structure in aspen forests. Journal of Field Ornithology 70:491–503.

Drumm, M. K. 1996. Fire history in the mixed conifer series of the Kings River Adaptive Management Area, Sierra National Forest. Thesis, Humboldt State University, Arcata, California, USA.

Emlen, J. T. 1970. Habitat selection by birds following a forest fire. Ecology 51:343–345.

Erwin, W. J., and R. H. Stasiak. 1979. Vertebrate mortality during the burning of reestablished prairie in Nebraska. American Midland Naturalist 10:247–249.

Finch, D. M., J. L. Ganey, W. Yong, R. T. Kimball, and R. Sallabanks. 1997. Effects and interactions of fire, logging, and grazing. Pages 103–136 *in* W. M. Block and D. M Finch, editors. Songbird ecology in Southwestern ponderosa pine forests: a literature review. U.S. Forest Service General Technical Report RMRS-292, Fort Collins, Colorado, USA.

Finney, M. A., C. W. McHugh, and I. C. Grenfell. 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. Canadian Journal of Forest Research 35:1714–1722.

Garrison, B. A., R. L. Wachs, J. S. Jones, and M. L. Triggs. 2002. Some factors influencing seedling density of California black oak (*Quercus kelloggii*) in the central Sierra Nevada, California. Madroño 49:115–121.

Gibbens, R. P., and H. F. Heady. 1964. The Influence of Modern Man on the Vegetation of Yosemite Valley. Division of Agricultural Sciences, University of California, Berkeley, California, USA.

Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. U.S. Forest Service General Technical Report RMRS-120, Fort Collins, Colorado, USA.

Granholm, S. L. 1982. Effects of surface fires on birds and their habitat associations in Coniferous Forests of the Sierra Nevada, California. Dissertation, University of California, Davis, USA.

Greeley. W. B., 1920. 'Piute forestry' and the fallacy of light burning. The Timberman March: 38–39. Reprinted *in* Forest History Today, Spring 1999: 33–37.

Grinnell, J., and T. Storer. 1924. Animal life in the Yosemite. University of California Press, Berkeley, California, USA.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, Inc., New York, New York, USA.

Hutto, R. L. 2008. The ecological importance of severe fires: some like it hot. Ecological Applications 18:1827–1834.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Jarvinen, O., and R. A. Vaisanen. 1975. Estimating relative densities of breeding birds by the line transect method. Oikos 26:316–322.

Johnson, D. H. 2007. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857–868.

Kilgore, B. M. 1971. Response of breeding bird populations to habitat changes in a giant sequoia forest. American Midland Naturalist 85:135–152.

Kilgore, B. M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. Pages 58–89 *in* H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. Proceedings of the conference on fire regimes and ecosystem properties. U.S. Forest Service General Technical Report WO-26, Washington, D.C., USA.

Kirkpatrick, C., C. J. Conway, and P. B. Jones. 2006. Distribution and relative abundance of forest birds in relation to burn severity in southeastern Arizona. Journal of Wildlife Management 70:1005–1012.

Kotliar, N. B., S. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25:49–64.

Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in Southwestern montane forests along a burn severity gradient. Ecological Applications 17:491–507.

Kruse, A., and J. Piehl. 1986. The impact of prescribed burning on ground-nesting birds. Pages 153–156 *in* G. Clambey and R. Pemble, editors. The prairie: past, present and future. Proceedings of the 9th North American Prairie Conference, Moorhead, MN. Center for Environmental Studies, Tri-College University, Fargo, North Dakota, USA.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA: <http://www.umt.edu/bbird/protocol/> Accessed 15 Feb 2001.

McClaran, M. P., and J. W. Bartolome. 1989. Fire-related recruitment in stagnant *Quercus douglasii* populations. Canadian Journal of Forest Research 19:580–585.

Minnich, R. A., M. G. Barbour, J. H. Burk, and R. F. Fernau. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. Conservation Biology 9:902–914.

Minnich, R. A., M. G. Barbour, J. H. Burk, and J. Sosa-Ramirez. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. Journal of Biogeography 27:105–129.

Morissette, J. L., T. P. Cobb, R. M. Brigham, and P. C. James. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research 32:2169–2183.

Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21–33.

Petersen, K. L., and L. B. Best. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. Wildlife Society Bulletin 15:317–329.

Pollet, J., and P. N. Omi. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. International Journal of Wildland Fire 11:1–10.

Purcell, K. L., and D. A. Drynan. 2008. Use of hardwood tree species by birds nesting in Ponderosa pine forests. Pages 417–431 *in* A. Merenlender, D. D. McCreary, and K. L. Purcell, technical editors. Proceedings of the sixth symposium on oak woodlands: today's challenges, tomorrow's opportunities. U.S. Forest Service General Technical Report, PSW-217, Albany, California, USA.

Raphael, M. G., M. L. Morrison, and M. P. Yoder-Williams. 1987. Breeding bird population during twenty-five years of post-fire succession in the Sierra Nevada. Condor 89:614–626.

Reinhardt, E. D., R. E. Keane, D. E. Calkin, and J. D. Cohen. 2008. Objectives and considerations for wildland fuel treatment in forest ecosystems of the interior western United States. Forest Ecology and Management 256:1997–2006.

Robel, R. J., J. P. Hughes, S. D. Hull, K. E. Kemp, and D. S. Klute. 1998. Spring burning: resulting avian abundance and nesting in Kansas CRP. Journal of Range Management 51:132–138.

Rodewald, A. D. 2003. Decline of oak forests and implications for forest wildlife conservation. Natural Areas Journal 23:368–371.

Russell, R. E., J. A. Royle, V. A. Saab, J. F. Lehmkuhl, W. M. Block, and J. R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian response to prescribed fire. Ecological Applications 19:1253–1263.

Saab, V. A., and H. D. W. Powell. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30:1–13.

Saab, V., W. Block, R. Russell, J. Lehmkuhl, L. Bate, and R. White. 2007. Birds and burns in the interior West: descriptions, habitats, and in Western forests. U.S. Forest Service General Technical Report, PNW-712, Portland, Oregon, USA.

Siegel, R. B., and D. F. DeSante. 1999. The draft avian conservation plan for the Sierra Nevada Bioregion: conservation priorities and strategies for safeguarding Sierra bird populations, Version 1.0. Institute for Bird Populations report to California Partners in Flight, Point Reyes, Station, California, USA.

Small, A. S. 1994. California birds: their status and distribution. Ibis Publishing, Vista, California, USA.

Smucker, K. M. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

U.S. Biological Survey. 1922. Fires in timber destroy much valuable wild life. Wilson Bulletin 1922:235–236.

U.S. Park Service. 2003. Fire monitoring handbook. Fire Management Program Center, National Interagency Fire Center, Boise, Idaho, USA.

Underwood, A. J. 1993. The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Australian Journal of Ecology 18:99–116.

Vankat, J. L., and J. Major. 1978. Vegetation changes in Sequoia National Park, California. Journal of Biogeography 5:377–402.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2:247–302.

White, D. H., B. R. Chapman, J. H. Brunjes, IV, R. V. Roftovich, Jr., and J. T. Seginak. 1999. Abundance and reproduction of songbirds in burned and unburned pine forests of the Georgia Piedmont. Journal of Field Ornithology 70:414–424.

Wiens, J. A., and J. T. Rotenberry. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Journal of Applied Ecology 22:655–668.

Wilson, C. W., R. E. Master, and G. A. Bukenhofer. 1995. Breeding bird response to pine-grassland community restoration for red-cockaded woodpeckers. Journal of Wildlife Management 59:56–67.

Woinarski, J. C. Z. 1990. Effects of fire on the bird communities of tropical woodlands and open forest in northern Australia. Australian Journal of Ecology 15:1–22.

Associate Editor: Robert Steidl.

APPENDIX

List of common and scientific names and guild assignment for bird species with total count >10 from 2001 to 2003 in Sierra National Forest, California, USA.

Common name	Scientific name	Nesting guild[a]	Migratory status[b]	Habitat association[c]	Foraging guild[d]
Mountain quail	*Oreotyx pictus*	GN	RS	PA	UF
Band-tailed pigeon	*Columba fasciata*	LN	SD	OA	CF
Mourning dove	*Zenaida macroura*	NA	RS	PA	UF
White-throated swift	*Aeronautes saxatalis*	NA	LD	PA	AF
Anna's hummingbird	*Calypte anna*	NA	SD	NA	UF
Belted kingfisher	*Ceryle alcyon*	NA	SD	RA	NA
Acorn woodpecker	*Melanerpes formicivorus*	SN	RS	OA	CF
Red-breasted sapsucker	*Sphyrapicus ruber*	SN	NA	RA	BF
Downy woodpecker	*Picoides pubescens*	SN	RS	RA	BF
Hairy woodpecker	*Picoides villosus*	SN	RS	CA	BF
White-headed woodpecker	*Picoides albolarvatus*	SN	RS	CA	BF
Northern flicker	*Calaptes auratus*	SN	SD	PA	UF
Pileated woodpecker	*Dryocopus pileatus*	SN	RS	CA	BF
Olive-sided flycatcher	*Contopus cooperi*	HN	LD	PA	AF
Western wood-pewee	*Contopus sordidulus*	HN	LD	OA	AF
Hammond's flycatcher	*Empidonax hammondii*	HN	LD	CA	AF
Dusky flycatcher	*Empidonax oberholseri*	LN	LD	PA	AF
Pacific-slope flycatcher	*Empidonax difficilis*	LN	LD	RA	AF
Black phoebe	*Sayornis nigricans*	NA	NA	RA	AF
Cassin's vireo	*Vireo cassinii*	LN	LD	RA	CF
Hutton's vireo	*Vireo huttoni*	LN	RS	OA	CF
Warbling vireo	*Vireo gilvus*	HN	LD	OA	CF
Steller's jay	*Cyanocitta stelleri*	LN	RS	CA	NA
Common raven	*Corvus corax*	HN	RS	NA	NA
Mountain chickadee	*Poecile gambeli*	SN	RS	CA	CF

(*Continued*)

APPENDIX. (*Continued*)

Common name	Scientific name	Nesting guild[a]	Migratory status[b]	Habitat association[c]	Foraging guild[d]
Bushtit	*Psaltriparus minimus*	LN	RS	NA	NA
Red-breasted nuthatch	*Sitta canadensis*	SN	RS	CA	BF
Brown creeper	*Certhia americana*	SN	RS	CA	BF
Winter wren	*Troglodytes troglodytes*	NA	RS	RA	UF
American dipper	*Cinclus mexicanus*	NA	RS	RA	NA
Golden-crowned kinglet	*Regulus satrapa*	HN	RS	CA	CF
Ruby-crowned kinglet	*Regulus calendula*	NA	LD	NA	CF
Townsend's solitaire	*Myadestes townsendi*	LN	SD	PA	NA
Hermit thrush	*Catharus guttatus*	LN	LD	CA	UF
American robin	*Turdus migratorius*	LN	SD	RA	UF
Wrentit	*Chamaea fasciata*	LN	RS	NA	UF
Cedar waxwing	*Bombycilla cedrorum*	NA	SD	NA	NA
Orange-crowned warbler	*Vermivora celata*	NA	LD	RA	CF
Nashville warbler	*Vermivora ruficapilla*	GN	LD	OA	CF
Yellow-rumped warbler	*Dendroica coronata*	HN	LD	CA	CF
Black-throated gray warbler	*Dendroica nigrescens*	LN	LD	OA	CF
Townsend's warbler	*Dendroica townsendi*	NA	LD	NA	CF
Hermit warbler	*Dendroica occidentalis*	HN	LD	CA	CF
MacGillivray's warbler	*Oporornis tolmiei*	LN	LD	CA	UF
Wilson's warbler	*Wilsonia pusulla*	LN	LD	RA	UF
Western tanager	*Piranga ludoviciana*	HN	LD	CA	CF
Spotted towhee	*Pipilo maculatus*	GN	RS	PA	UF
Chipping sparrow	*Spizella passerina*	LN	NA	PA	UF
Song sparrow	*Melospiza melodia*	GN	SD	PA	UF
Dark-eyed junco	*Junco hyemalis*	GN	SD	PA	UF
Black-headed grosbeak	*Pheucticus melanocephalus*	LN	LD	NA	CF
Brown-headed cowbird	*Molothrus ater*	NA	SD	PA	UF
Pine siskin	*Carduelis pinus*	NA	NA	CA	CF
Purple finch	*Carpodacus purpureus*	HN	SD	CA	CF

[a] Nesting guilds: SN, snag nesting; GN, ground nesting; LN, low nesting; HN, high nesting; NA, no assignment.
[b] Migratory status: LD, long distance migrant; SD, short-distance migrant; RS, resident.
[c] Habitat associations: CA, conifer associated; OA, oak associated; RA, riparian associated; PA, open-forest associated.
[d] Foraging guilds: AF, aerial foraging; CF, canopy foraging; UF, understory foraging; BF, bark foraging.