

Prescribed Fire Effects on Wintering, Bark-Foraging Birds in Northern Arizona

THERESA L. POPE,^{1,2} *United States Forest Service Rocky Mountain Research Station, 2500 S Pine Knoll Drive, Flagstaff, AZ 86001, USA*

WILLIAM M. BLOCK, *United States Forest Service Rocky Mountain Research Station, 2500 S Pine Knoll Drive, Flagstaff, AZ 86001, USA*

PAUL BEIER, *School of Forestry, Northern Arizona University, P.O. Box 15018, Flagstaff, AZ 86011, USA*

ABSTRACT We examined effects of prescribed fire on 3 wintering, bark-foraging birds, hairy woodpeckers (*Picoides villosus*), pygmy nuthatches (*Sitta pygmaea*), and white-breasted nuthatches (*S. carolinensis*), in ponderosa pine (*Pinus ponderosa*) forests of northern Arizona, USA. During winters of 2004–2006, we compared bird density, foraging behavior, and bark beetle activity among burned treatment and unburned control units. Hairy woodpecker density was 5 times greater in burn units, whereas white-breasted nuthatches and pygmy nuthatches had similar densities between treatments. Compared to available trees, trees used by foraging hairy woodpeckers had 9 times greater odds of having bark beetles in control units and 12 times greater odds in burn units. Tree diameter appeared to be the main factor bark-foraging birds used in selecting winter foraging trees. Our results suggest that forest managers can use prescribed fire treatments without detrimental effects to wintering nuthatches, while providing additional food to hairy woodpeckers. (JOURNAL OF WILDLIFE MANAGEMENT 73(5):695–700; 2009)

DOI: 10.2193/2007-537

KEY WORDS Arizona, bark-foraging birds, hairy woodpecker, *Picoides villosus*, prescribed fire, pygmy nuthatch, *Sitta carolinensis*, *Sitta pygmaea*, white-breasted nuthatch, winter.

Fire was the dominant natural disturbance agent in ponderosa pine (*Pinus ponderosa*) forests in northern Arizona, USA, until fire suppression efforts began in the early 20th century. Frequent, low-intensity fires were part of the ecology and evolutionary history of ponderosa pine forests (Cooper 1960, Covington and Moore 1994, Swetnam and Baison 1996, Moir et al. 1997). These fires produced a landscape mosaic of burned and unburned patches (Fulé et al. 1997). In an effort to return fires such as these to the landscape, forest managers are evaluating alternate forest management strategies that include using prescribed fire in fuel reduction and forest restoration treatments.

Because prescribed fires generally behave differently than wildfires, prescribed fires may produce different effects on wildlife and associated habitats. Studies investigating effects of fire on wintering birds are few (Blake 1982, Kreisel and Stein 1999, Bock and Block 2005, Covert-Bratland et al. 2006), especially for prescribed fire (King et al. 1998). However, winter may be a crucial time for resident birds because food is generally limited, insects are not as abundant, and many plants are dormant. As a result, food is patchily distributed and birds adopt a more opportunistic foraging ecology (Willson 1971, Crockett and Hansley 1978, Brawn et al. 1982, Morrison et al. 1986, Szaro et al. 1990). Also, winter habitat requirements might be different than breeding habitat requirements, because winter habitat must provide food as well as shelter from harsh conditions (Fretwell 1972; Grubb 1975, 1977; Conner 1979; Graber and Graber 1983). As such, winter survival can affect

populations, because birds that survive winter are available for reproduction the following breeding season (Fretwell 1972, Kreisel and Stein 1999). Therefore, increased knowledge on effects of prescribed fire on wintering, bark-foraging birds should lead to ecologically sound fire-management policies (Kotliar et al. 2005).

We investigated effects of prescribed fire on 3 wintering, bark-foraging birds in ponderosa pine forests of northern Arizona: hairy woodpeckers (*Picoides villosus*), white-breasted nuthatches (*Sitta carolinensis*), and pygmy nuthatches (*S. pygmaea*). These species are conspicuous, common winter residents in the area known to forage on bark beetles (Family Scolytidae; Beal 1911, Stallcup 1968, Anderson 1976). We compared bird density, foraging behavior, and bark beetle activity in burned and unburned control units in ponderosa pine forests of northern Arizona during winters of 2004–2006, the first 2 winters after all burn units were treated by prescribed fire. Bark beetles, which are known to increase activity in burned areas, could provide more food for bark-foraging birds (Ferrell 1996, McCullough et al. 1998, Bradley and Tueller 2001, Wallin et al. 2003, McHugh et al. 2003). Therefore, we expected an increase in bark-foraging bird density and a difference in foraging patterns in burn units as compared to control units after prescribed fire treatments.

STUDY AREA

We located one study site in the Coconino National Forest and one in the Kaibab National Forest, as part of the Birds and Burns Network. Ponderosa pine was the dominant overstory tree on the Kaibab study units. Pinyon pine (*Pinus edulis*), one-seed (*Juniperus monosperma*), and alligator (*J. deppeana*) junipers occurred on the control units but contributed little to stand canopies. Ponderosa pine also

¹ E-mail: tlpope@neo.tamu.edu

² Present address: Department of Wildlife and Fisheries Sciences, Texas A&M University, 210 Nagle Hall, College Station, TX 77843-2258, USA

Table 1. Description of study units on the Coconino and Kaibab National Forests, Arizona, USA, in 2004–2005, treatment (burn and control), area (ha), number of trees surveyed (*n*), average ($\pm$ SE) diameter at breast height (cm), and average ($\pm$ SE) tree height (m).

Treatment	Kaibab						Coconino					
	Area	<i>n</i>	dbh		Ht		Area	<i>n</i>	dbh		Ht	
			$\bar{x}$	SE	$\bar{x}$	SE			$\bar{x}$	SE	$\bar{x}$	SE
Burn	369	758	33.7	0.5	13.7	0.2	405	1940	23.1	0.2	12.7	0.1
Control	487	872	33.3	0.4	11.3	0.1	404	1567	24.5	0.3	10.9	0.1

dominated the overstory on the Coconino study units, with Gambel oak (*Quercus gambelii*) contributing to canopy structure. Alligator juniper was also found on both Coconino units. Open grassland patches in all locations were dominated by bunchgrass species, including Arizona fescue (*Festuca arizonica*) and blue gramma (*Bouteloua gracilis*). Topography on the Kaibab was flat, with elevations ranging from 2,100 m to 2,300 m, whereas topography on the Coconino varied from flat to steep hills, with elevations ranging from 2,070 m to 2,160 m.

METHODS

Each study site had a burn treatment unit paired with 1 or 2 control units of similar forest structure (Table 1). We chose treatment units nonrandomly in consultation with district fire managers on each forest. We then placed control units in representative areas with similar stand structures within 1 km of the treatment unit where no management was planned.

United States Forest Service personnel administered prescribed fires during autumn 2003 on the Coconino and during autumn 2003 and spring 2004 on the Kaibab (Table 2), a full growing season before we began collecting data. Fire personnel used ground-based ignition methods, with head, backing, and flanking fires at the unit edge and strip pattern or spot fires at the interior (Dickson 2006). All prescriptions were characterized as broadcast burns with expected fire behaviors of low to moderate intensity (Dickson 2006). Objectives of fire treatments included wildfire threat and hazardous fuels reduction, maintenance of natural fuel breaks, and restoration of natural ecological systems (Dickson 2006).

Our prescribed fires were heterogeneous in severity, with areas that were not burned at all, contrasted with areas where burns were severe enough to kill some trees. We quantified maximum bole char height, percent of the bole circumference that was charred at the base, and percent of

needles scorched as measures of fire activity that fire managers can incorporate into fire prescriptions. Average ($\pm$ SE) maximum bole char height for burn units was $1.2 \text{ m} \pm 0.04$. Average percent of the bole circumference that was charred at the base was 65.0 ± 0.81 and average percent of needles scorched was 6.6 ± 0.39 (Table 2). These values represent low-intensity fires that had little effect on forest structure.

Surveys

We estimated avian densities in each unit using point-transect distance sampling (Buckland et al. 2001). We randomized placement of the first point-count station and then assigned the other point-count stations in a systematic random sampling design using a Geographic Information System algorithm (see Dickson 2006 for more detail). The Kaibab study site had 40 point-count stations in the burn unit and 50 point-count stations in the control units. The Coconino study site had 40 point-count stations per treatment unit. Therefore, there were 170 point-count stations (80 in burn units and 90 in control units). Stations were approximately 300 m apart and ≥ 200 m from unit edges. At each station, we recorded direction and distance to each bird in distance categories (0–10 m, 11–25 m, 26–50 m, 51–75 m, and 76–100 m) during a 5-minute survey period. Point counts began within 30 minutes of sunrise and concluded within 5 hours. During winter, bird detectability on point counts does not decrease appreciably during these hours (Rollfinke and Yahner 1990, Gutzwiller 1993). We did not count in windy or wet (more than a light snow) conditions. We counted each station 8 times (4/season) between mid-October and mid-March, 2004–2006.

We estimated bird densities using Program DISTANCE 5.0 (Thomas et al. 2005). We used the conventional distance-sampling analysis engine. For each of our 3 focal species, we ran 3 models, each key function with the cosine series expansion (i.e., uniform + cosine, half-normal + cosine, and hazard-rate + cosine), poststratified estimates by

Table 2. Measurements of fire effects (max. bole char ht [m], % of needles scorched, and % of bole charred) from prescribed fires in 2003 and 2004 on each burn unit and burn units combined on the Coconino and Kaibab National Forests in northern Arizona, USA.

National forest	Dates burned	Max. bole char ht (m)		% of needles scorched		% of bole charred	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Kaibab	27 Oct 2003, 6 Nov 2003, 25 Mar 2004	2.6	0.11	17.6	1.05	85.8	1.01
Coconino	15 Sep 2003, 18 Sep 2003, 19 Sep 2003	0.7	0.02	2.3	0.29	56.9	1.00
Combined		1.2	0.04	6.6	0.39	65.0	0.81

treatment level, and chose the model with the lowest Akaike's Information Criterion (AIC).

We surveyed trees for signs of bark beetle activity using 10-m-radius circular subplots (0.03 ha) at each point-count station. We had 4 subplots: 1 at the station center and 3 within 100 m of the station center. To locate the 3 subplots, we assigned one a random bearing and distance from the station center (between 20 m and 90 m to prevent overlap with center plot and remain within 100-m radius of station center), using a random number table. We offset the 2 subplots from the first by 120° and 240°, respectively, and assigned each a distance from a random number table. We determined presence or absence of bark beetles in each ponderosa pine >12.7 cm diameter at breast height by noting evidence of bark beetle activity (i.e., pitch tubes, frass, boring dust, and fading needles) and woodpecker foraging (i.e., bark flaking, hole drilling). We also recorded diameter at breast height, maximum bole char height, percent of bole circumference charred at base, and percent of needles scorched for each tree (U.S. Department of the Interior National Park Service 2003).

We observed foraging activities of hairy woodpeckers, pygmy nuthatches, and white-breasted nuthatches from mid-October until mid-March, 2004–2006. At each point-count station, we searched the area within a 100-m radius of the station for foraging birds for 8 minutes. Once we located a bird, we watched the bird for 10 seconds before beginning an observation, which allowed the bird to resume normal activity patterns after being disturbed and also prevented only recording conspicuous behavior (Noon and Block 1990). For the first foraging event (e.g., a woodpecker pecking the tree) we observed after 10 seconds, we recorded diameter at breast height, maximum bole char height, percent of bole circumference charred at base, and percent of needles scorched for the tree where the foraging event occurred, as well as evidence of bark beetle activity. We observed foraging activities for all 3 focal species beginning at sunrise and concluding within 5 hours, visiting all stations equally throughout the season over both winters.

We examined how tree diameter (dbh), fire effects (e.g., max. bole char ht), bark beetle activity, and foraging behavior of bark-foraging birds in winter were related in each treatment by species using log-linear analysis (Noon and Block 1990, Agresti 1996). Log-linear models are examples of generalized linear models that do not distinguish between response and explanatory variables, treating all variables jointly as responses (Agresti 1996). Therefore, log-linear analysis applies when there is >1 response variable (Agresti 1996). We used log-linear models to study association patterns among 2 response variables, bark beetle activity and trees selected for foraging.

For each species, sample size for log-linear analysis included trees surveyed during bark beetle surveys in addition to trees where we observed foraging events (i.e., forage tree). For hairy woodpeckers, we examined 2,769 trees in burn units and 2,473 in control units. For pygmy nuthatches, we examined 2,773 and 2,506 trees, respectively;

whereas we examined 2,794 and 2,523 trees, respectively, for white-breasted nuthatches. We used 4 variables as factors: foraging behavior (F; i.e., a tree sampled in the bark beetle survey vs. where a foraging event occurred), bark beetle activity (B), maximum bole char height (C), and diameter at breast height (D), with each of these variables consisting of ≥ 2 categories. We only included the maximum bole char-height variable in the burn treatment analyses because all trees in the control units were in category 0. Using SPSS for Windows Release 15.0.0 (SPSS Inc., Chicago, IL), we began with a saturated model that included all main effects and possible interactions, then used backward elimination (using $\alpha = 0.05$ as probability for removal) to determine the final model. Goodness-of-fit of the final model is represented by the likelihood ratio (G^2), where low P -values represent poor model fit.

RESULTS

During 2 winter seasons of distance sampling, we detected hairy woodpeckers 160 times (47 in control units and 113 in burn units), white-breasted nuthatches 406 times (209 and 197, respectively), and pygmy nuthatches 678 times (337 and 341, respectively). We estimated density for hairy woodpeckers and white-breasted nuthatches using separate detection functions for each treatment level (burn vs. control) and for pygmy nuthatches using a global detection function for both treatment levels combined. Models including year offered no improvement over those with both years combined; therefore, we modeled density with observations pooled across years. For hairy woodpeckers and white-breasted nuthatches, the top 2 models had $\Delta\text{AIC} < 2$; therefore, we used model-averaging to estimate densities (Buckland et al. 2001). For pygmy nuthatches, only the half-normal + cosine model had $\Delta\text{AIC} < 2$, so we used the density estimate given by this model.

Hairy woodpecker density ($D/100 \text{ ha} \pm \text{SE}$) in the burn units (10.8 ± 2.0) was 5 times the density in control units (2.1 ± 0.3). Pygmy and white-breasted nuthatches had similar densities between burn and control units, pygmy nuthatches having densities of 45.0 ± 7.5 in burn units and 39.7 ± 7.1 in control units and white-breasted nuthatches having 9.8 ± 0.9 and 11.6 ± 1.4 , respectively.

We surveyed 5,138 trees for bark beetle activity. Bark beetle activity was twice as great in burn units, with 9.9% of trees in burn units ($n = 2,699$) having signs of bark beetle activity compared to only 4.8% of trees in control units ($n = 2,439$) with signs of bark beetle activity. Odds ($\theta \pm$ asymptotic standard error [ASE]; Agresti 1996) that a tree had signs of bark beetle activity in burn units were 2.2 ± 0.11 times that of control units. Furthermore, 19.7% of trees in the Kaibab burn unit had signs of bark beetle activity, whereas only 6.1% trees in the Coconino burn unit did. Therefore, odds of a tree having signs of bark beetle activity on the Kaibab unit were 3.8 ± 0.13 times that of the Coconino burn unit.

During 2 seasons of winter foraging observations, we recorded 104 hairy woodpecker foraging events (70 in burn

Table 3. Difference in proportion of trees with bark beetle activity and odds ratios ($\pm$ asymptotic standard error [ASE]) between trees surveyed for bark beetles (survey tree) and trees where we observed foraging events (forage tree) during winter for hairy woodpeckers, white-breasted nuthatches, and pygmy nuthatches on burn and control units in northern Arizona, USA, 2004–2006.

Species	Treatment	Survey tree	Forage tree	Difference in proportion	SE	Odds ratio	ASE
Hairy woodpecker	Control	0.05	0.33	0.28	0.08	9.41	0.36
	Burn	0.10	0.57	0.47	0.06	12.09	0.21
White-breasted nuthatch	Control	0.05	0.07	0.02	0.03	1.51	0.41
	Burn	0.10	0.12	0.02	0.03	1.19	0.17
Pygmy nuthatch	Control	0.05	0.12	0.07	0.04	2.67	0.98
	Burn	0.10	0.12	0.02	0.04	1.26	0.23

units, 34 in control units), 179 white-breasted nuthatch foraging events (95 burn and 84 control), and 141 foraging events for pygmy nuthatches (74 burn and 67 control). Hairy woodpeckers were the only species whose forage trees had signs of bark beetle activity in greater proportion than trees surveyed for bark beetle activity in both treatments. In control units, odds of forage trees having signs of bark beetle activity were 9 times that of the trees surveyed for bark beetle activity (Table 3). Odds were even greater on burn units, with odds of having signs of bark beetle activity 12 times greater for forage trees than for surveyed trees (Table 3). For white-breasted nuthatches, odds of forage trees having signs of bark beetle activity were not greater than of trees surveyed for bark beetle activity in either treatment (Table 3). Odds of pygmy nuthatch forage trees having signs of bark beetle activity were not greater than surveyed trees having signs of bark beetle activity in the burn treatment. In control units, however, odds that pygmy nuthatches foraged on trees with signs of bark beetle activity were more than twice that of trees surveyed for bark beetles that showed signs of bark beetle activity (Table 3).

Bark-foraging birds selected trees for foraging based on different factors, depending on bird species and treatment. Hairy woodpeckers foraging in burn units selected trees based on interaction of bark beetle activity and tree diameter (Table 4). In control units, hairy woodpeckers selected trees based on bark beetle activity and tree diameter independently (Table 4). Pygmy nuthatches selected trees based on tree diameter in both treatment units (Table 4). In addition, pygmy nuthatches selected trees in control units based on bark beetle activity (Table 4), which is consistent with our foraging observation results. White-breasted nuthatches selected trees based on tree diameter in both treatments,

as well as the interaction of bark beetle activity and maximum bole char height in the burn units (Table 4). Most observations of foraging hairy woodpeckers, white-breasted, and pygmy nuthatches were on trees with diameter at breast height >30.5 cm (75%, 66%, and 82%, respectively; Table 5).

Factors associated with bark beetle activity varied by treatment. In control units, tree diameter interacted with bark beetle activity, whereas in burn units, bark beetle activity interacted with both tree diameter and maximum bole char height (Table 4). Number of trees with bark beetle activity was similar across the 3 maximum bole char-height categories, yet the greatest proportion (53%) when compared to total number of trees in each category was in category 2 (>3 m; Table 5). Tree diameter followed the same pattern with 94% of bark beetle activity in trees 13–61 cm diameter at breast height (Table 5).

DISCUSSION

Density and foraging behavior of bark-foraging birds differed in response to effects of prescribed fire. Fire treatments did not appear to have an effect on densities of pygmy or white-breasted nuthatches; however, density of hairy woodpeckers was higher on burn units than on control units. Therefore, although low to moderate surface fires might benefit hairy woodpeckers, these fires do not appear to be detrimental to pygmy and white-breasted nuthatches, which may be due to forest stand structure remaining essentially intact following lower intensity surface fires.

The proportion of trees with bark beetles was greater in burn units than control units during the first 2 winters following prescribed fire treatments. Therefore, even low-severity surface fires such as these may attract bark beetles that are already present in the area. Although forest managers may be concerned with possible bark beetle outbreaks associated with prescribed fire treatments, Breece et al. (2008) found low mortality of ponderosa pine (7.6% on burn units) associated with bark beetle attacks for Birds and Burns Network sites in Arizona and New Mexico.

Although hairy woodpeckers, pygmy nuthatches, and white-breasted nuthatches are known to use bark beetles as food in winter (Beal 1911, Stallcup 1968, Anderson 1976), only hairy woodpeckers appear to focus on this winter food source after prescribed fire in our study areas. Whereas pygmy and white-breasted nuthatches occasionally foraged on trees with bark beetle activity in greater

Table 4. Final log-linear models selected from backward elimination examining relationships between maximum bole char height (C), bark beetle activity (B), tree diameter (D), and foraging behavior (F) for hairy woodpeckers, pygmy nuthatches, and white-breasted nuthatches in northern Arizona, USA, during winters of 2004–2006.

Species	Treatment	Final model	Likelihood ratio
Hairy woodpecker	Burn	(FBD, BCD)	$G^2_{24} = 12.79, P = 0.97$
	Control	(FB, FD, BD)	$G^2_5 = 1.00, P = 0.96$
Pygmy nuthatch	Burn	(BCD, FD)	$G^2_{30} = 21.37, P = 0.88$
	Control	(FD, FB, BD)	$G^2_5 = 6.39, P = 0.27$
White-breasted nuthatch	Burn	(FBC, BCD, FD)	$G^2_{25} = 21.45, P = 0.67$
	Control	(FD, BD)	$G^2_6 = 6.46, P = 0.37$

Table 5. Percent of trees surveyed for bark beetles (survey trees) and where we observed foraging events (forage trees) by hairy woodpeckers, pygmy nuthatches, and white-breasted nuthatches during winter in each variable category by species and treatment in northern Arizona, USA, 2004–2006.

	Forage trees							
	Survey trees		Hairy woodpecker		Pygmy nuthatch		White-breasted nuthatch	
	Burn	Control	Burn	Control	Burn	Control	Burn	Control
Bark beetles								
No	90.0	95.2	42.9	67.6	87.8	88.1	88.4	92.9
Yes	10.0	4.8	57.1	32.4	12.2	11.9	11.6	7.1
Max. bole char ht (m)								
None	23.4	100.0	8.6	100.0	21.6	100.0	26.3	100.0
0.5–3.0	69.0	0.0	58.5	0.0	67.6	0.0	69.5	0.0
>3.0	7.6	0.0	32.9	0.0	10.8	0.0	4.2	0.0
Dbh (cm)								
0.0–2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2.6–12.7	1.6	0.1	5.8	0.0	1.4	0.0	2.2	1.2
12.8–30.5	70.4	65.4	23.2	17.6	21.6	11.9	34.4	31.0
30.6–45.7	20.6	26.6	34.8	44.1	39.2	38.9	34.4	33.3
45.8–61.0	6.1	6.4	21.7	26.5	23.0	34.3	17.2	21.4
>61.0	1.3	1.5	14.5	11.8	14.9	14.9	11.8	13.1

proportion than surveyed trees, only foraging hairy woodpeckers did so consistently. Nuthatches may not have foraged for bark beetles as often as woodpeckers due to nuthatches having a more diverse diet in winter, including seeds cached in bark of trees and insects gleaned from bark fissures and needles (Norris 1958, Stallcup 1968, Anderson 1976, McEllin 1979).

Tree diameter was the main factor in determining whether a tree was used for foraging in winter by our 3 focal species, with larger diameter trees being selected by foraging birds. Bark beetles were also associated with larger diameter trees, which may partly explain why hairy woodpeckers foraged in larger diameter trees. However, larger diameter trees may also be used in winter more than other seasons because these trees provide more protection from wind (Grubb 1975, 1977). Furthermore, larger diameter trees have bark with deeper furrows, providing places for nuthatches to cache seeds and hiding places for invertebrates these birds use as food (Otvos 1965, Travis 1977, Jackson 1979, Brawn et al. 1982, Weikel and Hayes 1999).

Winter habitat quality is probably as important to persistence of bird populations as breeding season habitat (Conner 1979). Therefore, birds foraging in winter are likely to use strategies that maximize efficient food acquisition to ensure survival during this critical period (Brawn et al. 1982). Bark-foraging birds taking advantage of the increase in bark beetles as a food source following prescribed fire during winter might contribute to greater individual survival and, therefore, result in more birds breeding the following season (Kreisel and Stein 1999). Thus, availability of winter food resources may affect species on the population level as well.

MANAGEMENT IMPLICATIONS

Even though low-intensity surface fires might not affect forest structure as much as wildfires, prescribed fires can also attract bark beetles. Whereas specific fire-intensity goals will depend on the objectives of fire treatment and species being

managed, forest managers can design fire prescriptions to account for some increase in bark beetle activity, thus providing additional food for hairy woodpeckers. Furthermore, because low-intensity fires do not appear to affect forest structure in ponderosa pine forests of northern Arizona, managers can use this tool without having a detrimental effect on resident bark-foraging birds in winters initially following prescribed fires.

ACKNOWLEDGMENTS

We thank V. Saab, B. Dickson, S. Vojta, N. Gwinn, C. Breece, N. Breece, S. Hurteau, K. Bratland, S. Stollery, P. Fulé, T. Sisk, D. Huebner, L. Doll, and the wildlife lab group in the Northern Arizona University School of Forestry for their assistance and constructive advice in many aspects of this project. We thank B. A. Collier and R. M. King for their statistical analysis advice. We also thank M. L. Morrison whose comments on previous versions greatly improved the quality of this manuscript.

LITERATURE CITED

- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons, New York, New York, USA.
- Anderson, S. H. 1976. Comparative food habits of Oregon nuthatches. *Northwest Science* 50:213–221.
- Beal, F. E. L. 1911. Food of the woodpeckers of the United States. U.S. Department of Agriculture Biological Survey Bulletin no. 37, Washington, D.C., USA.
- Blake, J. G. 1982. Influence of fire and logging on nonbreeding bird communities of ponderosa pine forests. *Journal of Wildlife Management* 46:404–415.
- Bock, C. E., and W. M. Block. 2005. Response of birds to fire in the American Southwest. U.S. Forest Service General Technical Report PSW-GTR-191, Fort Collins, Colorado, USA.
- Bradley, T., and P. Tueller. 2001. Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. *Forest Ecology and Management* 142:205–214.
- Brawn, J. D., W. H. Elder, and K. E. Evans. 1982. Winter foraging by cavity nesting birds in an oak-hickory forest. *Wildlife Society Bulletin* 10: 271–275.
- Breece, C. R., T. E. Kolb, B. G. Dickson, J. D. McMillin, and K. M.

- Clancy. 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. *Forest Ecology and Management* 225:119–128.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford, United Kingdom.
- Conner, R. N. 1979. Seasonal changes in woodpecker foraging methods: strategies for winter survival. Pages 95–105 in J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, New York, New York, USA.
- Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern ponderosa pine forest since white settlement. *Ecological Monographs* 30:129–164.
- Covert-Bratland, K. A., W. M. Block, and T. C. Theimer. 2006. Hairy woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. *Journal of Wildlife Management* 70:1379–1392.
- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *Journal of Forestry* 92:39–47.
- Crockett, A. B., and P. L. Hansley. 1978. Apparent response of *Picoides* woodpeckers to outbreaks of the pine bark beetle. *Western Birds* 9:67–70.
- Dickson, B. G. 2006. Multi-scale response of avian communities to prescribed fire: implications for fuels management and restoration treatments in southwestern ponderosa pine forests. Dissertation, Colorado State University, Fort Collins, USA.
- Ferrell, G. T. 1996. The influence of insect pests and pathogens on Sierra forests. Pages 1177–1192 in *Sierra Nevada Ecosystem Project: final report to Congress, Volume II: assessments and scientific basis for management options*. Centers for Water and Wildland Resources, University of California, Davis, USA.
- Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey, USA.
- Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7:895–908.
- Graber, J. W., and R. T. Graber. 1983. Expectable decline of forest bird populations in severe and mild winters. *Wilson Bulletin* 95:682–690.
- Grubb, T. C. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. *Condor* 77:175–182.
- Grubb, T. C. 1977. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland: horizontal adjustments. *Condor* 79:271–274.
- Gutzwiller, K. J. 1993. Refining the use of point counts for winter studies of individual species. *Wilson Bulletin* 105:612–627.
- Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pages 69–93 in J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, New York, New York, USA.
- King, T. G., M. A. Howell, B. R. Chapman, K. V. Miller, and R. A. Schorr. 1998. Comparisons of wintering bird communities in mature pine stands managed by prescribed burning. *Wilson Bulletin* 110:570–574.
- Kotliar, N. B., V. A. Saab, and R. L. Hutto. 2005. Fire on the mountain: birds and burns in the Rocky Mountains. U.S. Forest Service General Technical Report PSW-GTR-191, Albany, California, USA.
- Kreisel, K. J., and S. J. Stein. 1999. Bird use of burned and unburned coniferous forests during winter. *Wilson Bulletin* 111:243–250.
- McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology* 43:107–127.
- McEllin, S. M. 1979. Population demographics, spacing, and foraging behaviors of white-breasted and pygmy nuthatches in ponderosa pine habitat. Pages 301–329 in J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, New York, New York, USA.
- McHugh, C. W., T. E. Kolb, and J. L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32:510–522.
- Moir, W. H., B. Giels, M. A. Benoit, and D. Scurlock. 1997. Ecology of southwestern ponderosa pine forests. Pages 3–27 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 RM-GTR-292, Fort Collins, Colorado, USA.
- Morrison, M. L., K. A. With, and I. C. Timossi. 1986. The structure of a forest bird community during winter and summer. *Wilson Bulletin* 98:214–230.
- Noon, B. R., and W. M. Block. 1990. Analytical considerations for study design. *Studies in Avian Biology* 13:126–133.
- Norris, R. A. 1958. Comparative biosystematics and life history of the nuthatches *Sitta pygmaea* and *Sitta pusilla*. University of California Publications in Zoology 56:119–300.
- Otvo, I. S. 1965. Studies on avian predators of *Dendroctonus brevicornis* LeConte (Coleoptera: Scolytidae) with special reference to Picipidae. *The Canadian Entomologist* 97:1184–1199.
- Rollfinke, B. F., and R. H. Yahner. 1990. Effects of time of day and season on winter bird counts. *Condor* 92:215–219.
- Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. *Ecology* 49:831–843.
- Swetnam, T. W., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11–32 in C. D. Allen, editor. Proceedings of the Second La Mesa Fire Symposium, 29–30 March 1994, Los Alamos, New Mexico. U.S. Forest Service General Technical Report RM-GTR-286, Fort Collins, Colorado, USA.
- Szaro, R. C., J. D. Brawn, and R. P. Balda. 1990. Yearly variation in resource-use behavior by ponderosa pine forest birds. *Studies in Avian Biology* 13:226–236.
- Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2005. Distance 5.0. Release 3. Research Unit for Wildlife Population Assessment, University of St. Andrews, United Kingdom.
- Travis, J. 1977. Seasonal foraging in a downy woodpecker population. *Condor* 79:371–375.
- U.S. Department of the Interior National Park Service. 2003. Vegetation monitoring protocols. Pages 55–18 in *Fire monitoring handbook*. National Interagency Fire, Fire Management Program Center, Boise, Idaho, USA.
- Wallin, K. F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology* 32:652–661.
- Weikel, J. M., and J. P. Hayes. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern coast range of Oregon. *Condor* 101:58–66.
- Willson, M. F. 1971. A note on foraging overlap in winter birds of deciduous woods. *Condor* 73:480–481.

Associate Editor: Steidl.