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FACTORS INFLUENCING OCCUPANCY OF NEST CAVITIES IN RECENTLY BURNED FORESTS

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Abstract. Recently burned forests in western North America provide nesting habitat for many species of cavity-nesting birds. However, little is understood about the time frame and the variables affecting occupancy of postfire habitats by these birds. We studied factors influencing the occupancy and reuse of nest cavities from 1–7 years after fire in two burned sites of western Idaho during 1994–1999. Tree cavities were used for nesting by 12 species of cavity nesters that were classified by the original occupant (strong excavator, weak excavator, or nonexcavator) of 385 nest cavities. We used logistic regression to model cavity occupancy by strong excavators ($n = 575$ trials) and weak excavators ($n = 206$ trials). Year after fire had the greatest influence on occupancy of nest cavities for both groups, while site of the burn was secondarily important in predicting occupancy by strong excavators and less important for weak excavators. Predicted probability of cavity occupancy was highest during the early years (1–4) after fire, declined over time (5–7 years after fire), and varied by site, with a faster decline in the smaller burned site with a greater mosaic of unburned forest. Closer proximity and greater interspersion of unburned forest (15% unburned) may have allowed a quicker recolonization by nest predators into the smaller burn compared to the larger burn with few patches of unburned forest (4% unburned). In combination with time and space effects, the predicted probability of cavity occupancy was positively affected by tree and nest heights for strong and weak excavators, respectively.

Key words: burned forests, cavity-nesting birds, Lewis's Woodpecker, Melanerpes lewis, *nesting habitat,* Picoides, Pinus ponderosa.

Factores que Influencian la Ocupación de Cavidades de Nidificación en Bosques Recientemente Quemados

Resumen. Los bosques del oeste de América del Norte que han sido recientemente quemados proveen hábitat de nidificación para muchas especies de aves que nidifican en cavidades. Sin embargo, se sabe poco sobre el marco temporal y las variables que afectan la ocupación por parte de las aves de los hábitats luego del fuego. Entre 1994 y 1999, estudiamos los factores que influencian la ocupación y el uso repetido de las cavidades de nidificación entre 1 y 7 años luego del fuego, en dos sitios quemados en el oeste de Idaho. Las cavidades de los árboles fueron usadas para nidificar por 12 especies de aves, las que fueron clasificadas (385 cavidades) según el ocupante original (excavador fuerte, excavador débil y no excavador). Usamos regresión logística para modelar la ocupación de las cavidades por parte de excavadores fuertes ($n = 575$ pruebas) y débiles ($n = 206$ pruebas). El año luego del fuego tuvo la mayor influencia en la ocupación de las cavidades de nidificación para ambos grupos, mientras que el sitio de la quema tuvo una importancia secundaria en predecir la ocupación por parte de excavadores fuertes y menos importancia por parte de excavadores débiles. La probabilidad predicha de ocupación de las cavidades fue mayor durante los primeros años (1–4) luego del fuego, declinó con el tiempo (5–7 años luego del fuego) y varió entre sitios, con una disminución más rápida en el sitio quemado más pequeño que presentó un mayor mosaico de bosque no quemado. La proximidad y la mayor dispersión de bosques no quemados (15% no quemado) puede haber permitido una recolonización más rápida de los depredadores de nidos en el sitio quemado pequeño, comparado con el sitio quemado mayor que presentó pocos parches de bosque no quemado (4% no quemado). En combinación con los efectos de tiempo y espacio, la probabilidad predicha de ocupación de cavidades fue afectada positivamente por la altura de los árboles y de los nidos para los excavadores fuertes y débiles, respectivamente.

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INTRODUCTION

Many cavity-nesting birds are associated with recently burned forests of interior western North America. Burned forests have been described as ephemeral source habitats for some species of cavity-nesting birds because early postfire habitats provide an increase in nesting and foraging opportunities (Hutto 1995), and a reduced risk of nest predation compared to unburned forests (Saab and Vierling 2001). Fire creates snags, alters insect communities, eliminates foliage, and changes the size, abundance, and distribution of tree species across landscapes (Huff and Smith 2000, Kotliar et al. 2002). Such physical and biological changes after fire are rapid compared to systems undergoing succession with no recent disturbance. Thus, time since fire is expected to be an important influence on the patterns of nest use by cavity-nesting birds.

Duration of occupancy by cavity nesters varies among species, most likely because of differences in preferred prey availability, in addition to the size, distribution, and decay rate of snags. For example, Black-backed Woodpeckers (see Table 1 for scientific names) rapidly colonize stand-replacement burns within one to two years after fire (Murphy and Lehnhausen 1998, Dixon and Saab 2000). Within five years, however, they become rare, presumably due to declines in their preferred prey of larval bark (Scolytidae) and wood-boring (Cerambycidae and Buprestidae) beetles. In contrast, Lewis's Woodpecker can be abundant in both recent burns (2–4 years postfire; Saab and Vierling 2001), and older burns (10–25 years; Bock 1970, Linder and Anderson 1998). Aerial insectivores such as Lewis's Woodpeckers are attracted to recently burned forests (Bock 1970, Tobalske 1997) because vegetation regrowth after wildfire generally results in rapid increases of arthropod populations (Horst 1970, Best 1979, Many 1984).

Avian responses to fire vary not only with time since fire, but also with burn severity and size, landscape context of burns, and postfire salvage logging (Saab and Dudley 1998, Murphy and Lehnhausen 1998, Kotliar et al. 2002, Saab et al. 2002). Landscape context of fires potentially has profound effects on breeding distributions and the source-sink status of burned habitats (Saab and Vierling 2001). Large-scale stand-replacement burns that lack a mosaic with green forest may serve as ephemeral source habitats for some species of cavity-nesting birds. Mammalian and reptilian nest predators are likely absent or their numbers are reduced drastically in large, recently burned forests, possibly allowing for high nest survival and productivity of cavity-nesting birds (Saab and Vierling 2001).

Cavity-nesting bird communities that occupy burned forests are diverse in mode of cavity acquisition and in foraging strategies (Bock et al. 1978, Raphael and White 1984, Saab and Dudley 1998). Strong and weak excavator species, as well as nonexcavators, use burned forests for nesting habitat. Strong excavators (e.g., Black-backed Woodpecker) forage primarily in bark and wood, and typically excavate and occupy a new nest cavity every year (Dixon and Saab 2000, Aitken et al. 2002). In contrast, nonexcavators (e.g., Mountain Bluebird) are primarily aerial insectivores, and commonly reuse nest cavities in subsequent years (Aitken et al. 2002). Weak excavators can follow yet a different pattern. For example, Lewis's Woodpecker is a weak excavator that typically enlarges existing cavities and will usurp nests of other species (Tobalske 1997, Saab and Dudley 1998). Thus, diverse life histories and patterns of cavity use characterize the assemblage of cavity-nesting birds that occupy early postfire forests.

The importance of recently burned forests to a diverse community of breeding cavity-nesting birds is well known (Bock and Lynch 1970, Bock et al. 1978, Raphael and White 1984, Hutto 1995, Saab and Dudley 1998). What is not known, however, is the time period over which cavity nesters occupy these forests and the factors responsible for their continued use. In this study, we asked the question, Which factors most influence the occupancy of nest cavities created after fire? We approached this question by examining the use of nest cavities over a 6-year period following fire. We monitored newly excavated cavities and recorded occupancy or vacancy through the study period, and modeled occupancy as a function of temporal scale, spatial scale, and microhabitat features at the nest tree. We hypothesized that year (time since fire) and site characteristics (amount of unburned forest, size, and severity of the burn) would have the greatest effects on occupancy of nest cavities in burned forests.

TABLE 1. General patterns of cavity use in two burned forests of southwestern Idaho. Table indicates number of cavities used and number of nesting attempts made from 1994–1999, ordered by abundance of original occupants. Secondary cavity nesters were original occupants in rare cases when a cavity was excavated but not subsequently occupied by a primary cavity nester. These data were used to model occupancy of nest cavities throughout the study period.

	No. cavities as original occupant			Total nesting attempts		
Species	Foothills Burn	Star Gulch Burn	Total	Foothills Burn	Star Gulch Burn	Total
Lewis's Woodpecker *Melanerpes lewis*	86	35	121	141	54	195
Hairy Woodpecker *Picoides villosus*	39	67	106	40	68	108
Northern Flicker *Colaptes auratus*	25	45	70	26	47	73
Black-backed Woodpecker *Picoides arcticus*	9	30	39	9	30	39
Mountain Bluebird *Sialia currucoides*	6	10	16	11	21	32
Western Bluebird *Sialia mexicana*	11	6	17	28	11	39
White-headed Woodpecker *Picoides albolarvatus*	4	8	12	4	9	13
American Kestrel *Falco sparverius*	0	0	0	10	1	11
Pileated Woodpecker *Dryocopus pileatus*	0	2	2	0	2	2
Downy Woodpecker *Picoides pubescens*	0	1	1	0	1	1
Red-naped Sapsucker *Sphyrapicus nuchalis*	0	1	1	0	1	1
European Starling *Sturnus vulgaris*	0	0	0	3	0	3
Totals	180	205	385	272	245	517

METHODS

STUDY AREA

We studied cavity-nesting birds from 1994–1999 in two burned sites of southwestern Idaho (43°35′N, 115°42′W). Elevation ranged from 1130 to 2300 m and the perimeters of the burns were separated on average by 10 km. The Foothills Burn (89 159 ha) was created in August 1992 by a high-severity, stand-replacing wildfire. Most standing trees were killed by the fire, and green forest patches occupied less than 4% of the area within a 1-km radius of nest trees (Appendix). Postfire salvage logging was conducted in the Foothills Burn, and approximately half the snags over 23 cm diameter at breast height (dbh) were removed for timber harvest (Saab and Dudley 1998). The Star Gulch Burn (12 467 ha) was created in August 1994 by a mixed-severity, patchy wildfire that resulted in a mosaic of burned and green forest. In contrast to the Foothills Burn, patches of green forest occupied 15% of the landscape in the Star Gulch Burn (Appendix) and the site was not salvage logged. In both study sites, prefire tree canopy was dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), with inclusions of quaking aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), and Scouler's willow (*Salix scouleriana*). Trees and snags were often patchily distributed within the burned landscapes and interspersed with large openings of shrubs, including ninebark (*Physocarpus malvaceus*) and ceanothus (*Ceanothus velutinus*).

In order to model cavity occupancy, we needed to locate and monitor nests in both study sites throughout the 6-year study period, determine the original excavator of each cavity, record the history of cavity use starting with the first year of occupancy, measure nest tree characteristics, and characterize the landscape surrounding nest

TABLE 2. Summary of nest cavity reuse by cavity-nesting birds in burned forests of ponderosa pine and Douglas-fir in southwestern Idaho. The reuse patterns are based on 294 cavities with 398 nesting attempts.

Original occupant	No. nest attempts	Cavities physically surviving to following nest attempt (%)	Cavity reuse (%)			
			Not reused	By same species	By same guild[a]	By different guild
Strong excavators						
Northern Flicker	56	86	90	0	0	10
Pileated Woodpecker	1	100	100	0	0	0
White-headed Woodpecker	11	91	70	10	0	20
Red-naped Sapsucker	1	100	100	0	0	0
Hairy Woodpecker	89	81	68	3	0	29
Downy Woodpecker	1	100	100	0	0	0
Black-backed Woodpecker	29	76	73	0	0	27
Total	188	82	76	2	0	22
Weak excavators						
Lewis's Woodpecker	132	70	45	47	0	9
Nonexcavators						
American Kestrel	8	63	100	0	0	0
Western Bluebird	36	94	56	27	6	12
Mountain Bluebird	31	87	63	19	11	7
European Starling	3	100	67	33	0	0
Total	78	89	62	22	7	9
Overall total	398	79	64	19	2	15

[a] Excluding cavities reused by the same species.

trees. The following methods explain how these data were collected and incorporated into our modeling.

NEST SEARCHING AND MONITORING

We conducted a complete census of nest cavities in both study sites using belt transects (0.4 × 1.0 km) during May–June in an area that averaged 1852 ha each year (range 1582–2468 ha) from 1994–1999. During the study, we found 1096 cavities, of which we used 385 known-aged cavities for modeling occupancy because they were found during the first year of excavation, after the fire, and the original occupant was known (Table 1). Subsequent to finding newly excavated cavities, cavities were observed to determine occupancy during a minimum of two 20-min visits between early May and late June every year. Cavities in which eggs were laid were considered occupied; cavities without eggs were classified as vacant. Occupied cavities were monitored every 3–4 days until fledging or failure. Egg laying was determined by viewing adult behavior (90% of nests) that indicated incubation and by direct observation (10% of nests) using an electronic camera (Dudley and Saab 2003). The cavity viewer consisted of a monochrome pinhole camera with a light source mounted on the end of a telescoping pole. With the viewer, we monitored cavities up to 12 m high and with minimum cavity entrances of 3.5 cm. We used a handheld monitor on the ground to view the cavity contents. We do not know the extent to which individual birds may have occupied the same cavities in subsequent years because birds were not marked.

Ninety-one of the 385 cavities used to model occupancy were observed in only one year of the study and we could not determine if these cavities were reused. The remaining 294 cavities were observed in at least two consecutive years and had the potential for reuse. These cavities were used to describe reuse patterns (Table 2). Occupancy was evaluated as the response variable, whereas characteristics of reuse patterns were used as predictor variables, including the number of species using an individual cavity, percentage of nesting attempts that were in the same guild as the original occupant, and percentage of years that a cavity produced a successful nest (Table 3).

Species were placed into guilds according to their mode of cavity acquisition as a strong excavator, weak excavator, or nonexcavator, simi-

TABLE 3. Covariates used to model occupancy of nest cavities in recently burned forests of southwestern Idaho.

Covariate	Description
Decay	Decay class (0–5; Cline et al. 1980) of nest tree during year of cavity occupancy. 0 = live tree, 5 = most decayed tree
Diameter at breast height (dbh)	Diameter (cm) of nest tree in the first year of cavity occupancy
Cavity height	Height (m) of nest cavity
Tree height	Height (m) of nest tree
Number of species	No. of cavity-nesting species that occupied the cavity during the study period
Snag density	No. of snags and trees >23 cm dbh recorded in 11.3-m-radius plots (0.04 ha) centered at each nest tree in the first year of cavity occupancy
Orientation	Compass bearing in which the cavity entrance faced, placed in 6 categories: 1 = 0–60°; 2 = 61–120°; 3 = 121–180°; 4 = 181–240°; 5 = 241–300°; 6 = 301–359°
Precipitation	Cumulative precipitation (mm) for March–June for each year, recorded at a weather station on the periphery of the study area
Same guild	Percentage of nesting attempts by species in the same guild as the original occupant (strong-, weak-, or non-excavator)
Site	Site of the burn: Foothills or Star Gulch
Landscape context	Percentage of unburned forest within a 1-km radius of nest locations
Potential nest competition	Densities of nesting Lewis's Woodpeckers within a 300-m radius of nest locations
Year postfire	Year after fire in which a nest cavity was occupied or available for nesting. Full time model, each time interval is modeled individually (6 parameters, 1994–1999).
Postfire period	Temporal effect constrained to 1 parameter that groups cavity occupancy into 2 time periods: years 1–4 after fire and years 5–7 after fire (2 parameters including intercept)
Years successful	Percentage of years that an occupied nest cavity fledged at least one young

lar to those described by Martin et al. (2004) except that we classified Downy Woodpecker as a strong excavator. The only weak excavator in our study was Lewis's Woodpecker. These guilds were used to model occupancy (n = 385), and to summarize cavity reuse patterns (n = 294; Table 2).

A nest was considered successful if parents were observed feeding young near the time of fledging (80% of average fledging age for each species; Dudley and Saab 2003) or if fledged young were observed near the nest. We classified nest failures as depredated (based on loss of nestlings, predator signs on nest trees, or adult behavior), weather related, abandoned, or unknown.

NEST TREE AND STUDY SITE CHARACTERISTICS

For each nest, we recorded the following variables: tree decay class, diameter at breast height, cavity height, tree height, cavity orientation, snag density, number of species that occupied the cavity, percentage of nesting attempts by species in the same guild as the original occupant, and percentage of years that a nest cavity fledged young. Tree decay was classified from 0 to 5, representing increasing decay from live (0) to most decayed (5; Cline et al. 1980). Snag density was measured as the number of snags ≥23 cm dbh in a 0.04-ha circle around each nest tree.

We characterized study sites using two variables: landscape context and potential nest competition. Landscape context was measured as the mean percentage of unburned forest and mean snag densities surrounding nests in the two burns (Appendix). We used nesting densities of Lewis's Woodpecker to represent potential nest competition because this woodpecker is known to usurp nests of other cavity nesters (Tobalske 1997; Saab and Dudley, unpubl. data), potentially affecting the occupancy of individual nest cavities by other species. We georeferenced all nest locations and then used ArcView (ESRI 1999) to calculate nesting densities of Lewis's Woodpeckers within a 300-m radius (28 ha) of all nest trees. This area likely encompasses the territory of the species during the breeding season (see Bock 1970, Tobalske 1997). Mean densities were higher in the Foothills Burn than in the Star Gulch Burn ($t = 3.3$, $P < 0.001$; Appendix).

MODEL BUILDING, SELECTION, AND INFERENCE

We used logistic regression models (Hosmer and Lemeshow 2000) to model the probability of cavity occupancy by nesting birds that were classified into two groups based on their excavator guilds: (1) those initially occupied by strong excavators; and (2) those initially occupied by weak excavators. We attempted to model cavity occupancy of a third group, those with nonexcavators as original occupants, but results were inconclusive due to small sample size. We did not analyze our data as repeated measures because logisitic models fitted using nonlinear mixed procedures (SAS Institute 2000) indicated little evidence of spatial or temporal autocorrelation.

For each group, we generated an *a priori* set of candidate models composed of a fully parameterized, global model and its reduced forms containing biotic and abiotic factors that we hypothesized would most influence cavity occupancy based on previous studies (Raphael and White 1984, Nilsson 1984, Li and Martin 1991, Martin and Eadie 1999). The Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) was applied to the global models to assess whether they adequately fitted the data. We also calculated the overdispersion parameter, $\hat{c}$ (Pearson's χ^2 divided by the degrees of freedom; McCullagh and Nelder 1989), for the global models to further evaluate fit and to assess whether a quasi-likelihood correction was necessary (to adjust our results if $\hat{c} > 1.2$; Burnham and Anderson 2002). Further, we evaluated the deviance residuals from these models for strong evidence of temporal (year postfire and postfire period) or spatial (site) autocorrelation (Table 3).

For global models that fit the data adequately, we selected among candidate models by ranking them based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Hurvich and Tsai 1989). The difference between the AIC_c of a given candidate model and the one with the lowest AIC_c in the candidate set provided the ranking metric (ΔAIC_c). As a general guideline, ΔAIC_c between 0 and 2 indicates substantial support for that model being the best approximating model, ΔAIC_c between 4 and 7 represents considerably less support, and ΔAIC_c greater than 7 indicates essentially no support (Burnham and Anderson 2002). We report specific model results only for models with ΔAIC_c of approximately 2 or less because those are the ones best supported by the data (Anderson et al. 2001, Burnham and Anderson 2002).

Thirteen covariates were used in the models to evaluate which factors best predicted occupancy for 385 nest cavities (Table 3). Nest tree species was not included as a predictor variable because most (61%) occupied nest cavities were located in ponderosa pines (Appendix).

The site variable represented the two burned areas, Foothills and Star Gulch. Sites differed by several characteristics, including landscape context and potential nest competition (Appendix). These two variables could not be analyzed as individual covariates because they were highly correlated with site and we could not separate their effects from site effects.

Other factors used to model occupancy of nest cavities in relation to the study area included year after fire; year after fire grouped into two postfire periods, early (1–4 years) and late (5–7 years) postfire years; and annual precipitation (Table 3). This postfire period was used because of expected biological and physical changes during early postfire years. Numeric responses by bark and wood foraging bird species usually occur 1–2 years after fire and their numbers diminish by years 5 and 6 after fire (Bock et al. 1978, Apfelbaum and Haney 1981, Dixon and Saab 2000). The early years in the postfire period covariate represented 2–4 years after fire for the Foothills Burn and 1–4 years after fire for the Star Gulch Burn, whereas the later years represented 5–7 years after fire for the Foothills Burn and 5 years after fire for the Star Gulch Burn.

Nest success was monitored in years 1994–1997 for all species, and in years 1998–1999 for only three species: Lewis's, Black-backed, and White-headed Woodpeckers. We did not include the covariate describing percentage of years in which the cavity had a successful nest (Table 3) with the postfire-period models (early postfire years vs. later postfire years; Table 3) for the original occupant group of strong excavators because we only had data for 16% of the nesting attempts during years 1998–1999.

Other than the global model, models with a time factor did not include covariates representing precipitation because this abiotic factor had a time element inherent in the data (Appendix). Temperature (°C) was considered but not used as a covariate because the mean varied little throughout the 6-year study period (21.1 ± 1.4°C; $F = 0.1$, $P = 0.9$). Models for weak excavator (Lewis's Woodpecker) did not include number of species using an individual cavity or percentage of nesting attempts that were in the same guild as the original occupant because once this species occupied a nest cavity, it tended to occupy the cavity for several breeding seasons (Table 2).

We used PROC LOGISTIC to compute adjusted odds ratios and their 95% profile likelihood confidence intervals (SAS Institute 2000) to evaluate the magnitude of effect that each variable had upon cavity occupancy in top-fitting models. The adjusted odds-ratio estimate is based on raising the *i*th model coefficient (β_i) to base *e* (Hosmer and Lemeshow 2000). We interpreted an adjusted odds ratio for a continuous predictor variable >1 as the predicted odds of cavity occupancy for every 1-unit increase in the continuous variable. For adjusted odds ratios <1, we computed the reciprocal and evaluated it relative to predicted odds of vacancy. Adjusted odds ratio for a categorical predictor variable was interpreted in a similar manner except predicted odds related to one category level versus another. When a predictor variable contained >2 category levels, we chose one level as a logical reference and presented adjusted odds ratios relative to that category (e.g., probability of cavity occupancy appeared to change around 4 years postfire, so we presented odds ratios for this variable relative to year 4).

We present adjusted odds ratios because these estimates account for other variables in a model (Allison 1999). We used the lower bound or the upper bound of the 95% confidence interval as a minimum estimate of effect size, depending on whether an adjusted odds ratio was >1 or <1. Note that a predictor variable (or category level) may be considered statistically significant if this confidence interval does not contain 1. An adjusted odds ratio, however, may be statistically significant but ecologically unimportant in size (Yoccoz 1991), so we interpreted estimates within an ecological context.

RESULTS

Three hundred eighty-five cavities, constituting 517 nesting attempts, were used to model occupancy of nest cavities in burned forests during 1994–1999. Lewis's Woodpecker, Hairy Woodpecker, and Northern Flicker were the most abundant cavity-nesting species, comprising 73% of all nesting attempts (Table 1). Forty-seven percent of cavities and 53% of nesting attempts were recorded from the Foothills Burn, while 53% of cavities and 47% of nesting attempts were from the Star Gulch Burn (Table 1). Of the 517 nesting attempts analyzed, 44 were monitored in 1994, 90 in 1995, 102 in 1996, 133 in 1997, 74 in 1998, and 74 in 1999. Duration of individual cavity occupancy was variable but brief for most cavities, with 296 occupied for one nesting attempt, 57 occupied for two nesting attempts, 23 occupied for three attempts, seven occupied for four attempts, and two occupied for five attempts. Nesting attempts were generally ≥1 year apart, except in 26 cases (18 in Foothills Burn and eight in Star Gulch Burn) where cavities were reoccupied during the same year. Two species were responsible for creating nearly 70% of the cavities in our study area. Hairy Woodpeckers were the original excavator in most cases, 148 cavities (38% of the total), while Northern Flickers were the original excavator of 118 nests (31%).

We checked 294 of these 385 cavities in at least two consecutive years (Table 2, Fig. 1). Reuse patterns were described from these cavities, including their history of use by individual species and guilds. Such information provided context on the cavities used to model occupancy. Ten cavities were followed for all six years (i.e., five potential reuse cases per cavity), 30 for five years, 58 for four years, 68 for three years, and 124 for two sequential years. Four cavities were checked in only one year but were reused for nesting within that year. Sixty-four of the 294 cavities were physically destroyed after one year of occupancy; the remaining 230 cavities (89 reused and 141 not reused), constituting 316 nesting attempts, provided the basis for evaluating cavity reuse patterns (Table 2).

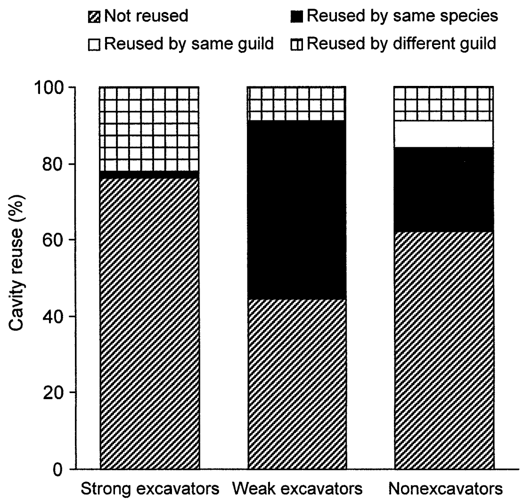

FIGURE 1. Reuse of nest cavities (%) in relation to cavity-nesting guild in ponderosa pine and Douglas-fir forests of southwestern Idaho. Sample sizes (nesting attempts) for strong excavators, weak excavators, and nonexcavators are n = 155, n = 92, and n = 69, respectively.

Cavities previously used by weak excavators (Lewis's Woodpecker) had the highest reuse rate (55%), followed by nonexcavators (38% reuse), and strong excavators (24% reuse; Table 2). Reuse by the same species was rare among strong excavators (2%), most frequent in weak excavators (47% for Lewis's Woodpecker), and intermediate for nonexcavators (22%; Fig. 1). Strong excavators (primarily *Picoides* spp.) provided the best nesting opportunities for weak excavators and nonexcavators (Fig. 1). Hairy Woodpecker cavities were used most often by a different guild (29%), followed by Black-backed Woodpecker (27%), White-headed Woodpecker (20%), and Northern Flicker cavities (10%; Table 2).

We contrasted 18 different models with various covariate combinations to predict the probability of occupancy for cavities initially occupied by strong excavators, and 18 models for those originally occupied by weak excavators (Table 4). For the set of models developed to predict cavity occupancy with the original occupant as strong excavator, there were 575 trials, of which 297 were occupied and 278 vacant. Of the occupied cavities (n = 297), 79% were only occupied by strong excavators, 11% by both strong and weak excavators, and 10% by both strong excavators and nonexcavators. Thus, the modeling of cavity occupancy was primarily for strong excavators and hereafter is referenced as probability of occupancy by strong excavators.

For the set of models developed to predict cavity occupancy with the original occupant as weak excavator, there were 206 trials, of which 163 were occupied and 43 vacant. Of the occupied cavities (n = 163), 96% were occupied only by weak excavators, 4% by both weak and nonexcavators, and $<$0.001% by both weak and strong excavators. Thus, this modeling of cavity occupancy was primarily for weak excavators and hereafter is referenced as probability of occupancy by weak excavators.

Goodness-of-fit tests indicated that global models for both strong (P = 0.84) and weak (P = 0.26) excavators adequately fitted the data. In addition, no strong temporal or spatial patterns were evident in the deviance residual plots for either global model, so we treated time and space as fixed effects. We did not apply a quasi-likelihood correction to the model ranking criterion (AIC_c) or to standard errors of parameter estimates because the overdispersion parameter estimates for the global models were close to one.

The best-fitting model for strong excavators was the only plausible one relative to others in the candidate set (Table 4; model 1, Akaike weight = 0.99). That is, the model containing year postfire, site, cavity orientation, tree decay, and tree height was at least 116 times more plausible than the next best model. Predicted probabilities of occupancy were most strongly influenced by year after fire and site, with occupancy higher in early postfire years and in the Foothills Burn. The odds of cavity occupancy were nearly 15 times higher during the first year after fire than during the fourth year postfire (Table 5, Fig. 2). Tree cavities in the Foothills Burn had at least 5.3 times higher odds of occupancy than cavities in the Star Gulch Burn (Table 5). Occupancy was less influenced but positively related to cavities with greater tree heights, with decay class 2, and with easterly orientations of 61–120° (Table 5, Fig. 2). The odds of vacancy were at least 1.2 times higher for cavities facing southwest (category 4 = 181–240°) than nest cavities facing an easterly direction (category 2; Table 5). The range of tree heights did not influence occupancy of strong excavators during early postfire years, whereas probability of occupancy increased with greater tree heights in later

TABLE 4. Model selection results based on logistic regression, used to predict cavity occupancy by strong excavators (n = 575 trials) and by a weak excavator (Lewis's Woodpecker; n = 206 trials) nesting in two recently burned areas of southwestern Idaho, 1994–1999. Models are ranked from most plausible ($\Delta AIC_c = 0$) to least plausible; k is the number of parameters. All models with $\Delta AIC_c \leq 2.04$ are listed, as well as the global model regardless of its plausibility. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best-fitting model compared to other models. See Table 3 for explanation of variable names.

Candidate model	Log likelihood	k	ΔAIC_c[a]	Akaike weight (w_i)	w_I/w_i
Strong excavators					
Model 1: Year postfire, Site, Orientation, Decay, Tree height	–290.28	19	0.00	0.99	1.0
Same guild, Year postfire, Postfire period, Years successful, Precipitation, Nest height, Number of species, Dbh, Site, Orientation, Decay, Tree height[b]	–286.35	27	9.52	<0.01	116.9
Weak excavators					
Model 1: Postfire period	–101.50	2	0.00	0.26	1.0
Model 2: Year postfire	–97.64	6	0.66	0.19	1.4
Model 3: Postfire period, Nest height	–101.09	3	1.24	0.14	1.9
Model 4: Year postfire, Years successful	–97.26	7	2.02	0.09	2.9
Model 5: Postfire period, Site	–101.49	3	2.04	0.09	2.9
Year postfire, Postfire period, Years successful, Precipitation, Nest height, Dbh, Site, Orientation, Decay, Tree height[b]	–88.62	21	17.21	<0.01	5454.2

[a] Strong excavators: minimum AIC_c = 619.93; weak excavators: minimum AIC_c = 207.05.
[b] Global model.

postfire years (Fig. 2). This pattern was particularly evident at the Star Gulch Burn, where the predicted probability of occupancy was below 0.5 at cavities with lower tree heights.

The best-fitting models for weak excavators (Lewis's Woodpecker) were the top five models, all of which included time effects (Table 4). All of these models had ΔAIC_c values $\leq$2.04, demonstrating that none of these models could be discounted as an explanation of occupancy by Lewis's Woodpecker. The sum of the Akaike weights for the models was 0.77, indicating that 77% of the weight of evidence for occupancy of nest cavities was in models 1–5. Predicted probability of occupancy was most strongly influenced by year after fire (Table 4), and less affected but positively related to cavities with greater nest heights and those with successful nests in most years (Fig. 3, 4). The effect of site was inconclusive by itself but was important in predicting cavity occupancy when included with postfire period (Table 4, Model 5). The odds of cavity occupancy by Lewis's Woodpecker were at least 1.4 times greater during early years (1–4) after fire than for later postfire years (5–7; Table 6, model 1). The predicted probability of occupancy appeared to decline through time, but was especially apparent by year 7 after fire (Fig. 4). The odds of a vacant cavity were at least 1.5 times higher during the seventh year postfire than during the fourth year postfire (Table 6, model 2). Probability of occupancy was high for cavities of various nest heights during early postfire years, whereas predicted probabilities increased with nest height in the later postfire years (Fig. 3). Regardless of the percentage of years with a successful nest, predicted probabilities of occupancy through the sixth year postfire were high (>0.6) compared to seven years after fire ($\leq$0.5; Fig. 4).

DISCUSSION

Time since fire had the greatest influence on occupancy of nest cavities for all species, whereas site characteristics were secondarily important in predicting cavity occupancy. Microhabitat features had an important but weaker influence than year or site on cavity occupancy. Of cavities for which we knew the original occupant, few were reused in subsequent years even among cavities used by nonexcavators. Reused cavities were located in taller, decayed trees, faced an easterly direction, were excavated higher in the tree, and tended to produce successful nests.

Cavities available to nonexcavators originated primarily from the 22% of reused cavities cre-

TABLE 5. Parameter estimates ± SE, and adjusted odds ratios from the best model (Table 4) for predicting probability of occupancy of nest cavities by strong excavators in recently burned forests of southwestern Idaho during 1994–1999. Odds ratios for categorical variables indicate the odds of occupancy for one category level relative to another category level (specified in ''contrast'' column). Odds ratios for continuous variables indicate the odds of occupancy for every 1-unit change in the variable. Confidence limits that do not contain 1 are considered statistically significant.

		Adjusted odds ratio		
Parameter Value	Parameter estimate ± SE	Contrast	Estimate	Confidence limits
Intercept	–0.92 ± 0.39			
Year postfire				
1	3.62 ± 0.73	1 vs. 4	64.2	15.0–490.2
2	2.21 ± 0.34	2 vs. 4	15.8	7.5–35.5
3	0.97 ± 0.25	3 vs. 4	4.6	2.6–8.1
5	–0.50 ± 0.25	5 vs. 4	1.1	0.6–1.9
6	–2.13 ± 0.45	6 vs. 4	0.2	0.07–0.6
7	–3.63 ± 0.61	7 vs. 4	<0.1	0.01–0.2
Site				
Foothills	1.13 ± 0.16	Foothills vs. Star Gulch	9.5	5.3–18.0
Orientation				
1	–0.04 ± 0.22	1 vs. 2	0.5	0.2–1.0
3	0.11 ± 0.23	3 vs. 2	0.6	0.3–1.2
4	–0.23 ± 0.25	4 vs. 2	0.4	0.2–0.8
5	–0.43 ± 0.27	5 vs. 2	0.3	0.1–0.7
6	–0.13 ± 0.21	6 vs. 2	0.4	0.2–0.9
Decay				
0	0.03 ± 1.14	0 vs. 2	0.5	0.02–6.0
1	0.38 ± 0.48	1 vs. 2	0.7	0.3–1.4
3	0.18 ± 0.44	3 vs. 2	0.6	0.3–1.2
4	–0.14 ± 0.58	4 vs. 2	0.4	0.1–1.3
5	–1.21 ± 1.19	5 vs. 2	0.1	<0.01–1.7
Tree height				
	0.05 ± 0.01		1.1	1.0–1.1

ated by strong excavators, while nearly 80% of excavated cavities were not reused. As the burns became older, the number of available cavities increased as a result of strong excavators (primarily Hairy Woodpeckers) creating new nest cavities every year through the study period. During the first two years after fire, numbers of cavity-nesting birds were relatively low (Saab and Dudley 1998). Their numbers doubled, however, within four years after the Foothills Fire, suggesting that suitable nest cavities were not limited in the later postfire years.

These results provide strong evidence for our hypotheses that year (time since fire) and site characteristics (amount of unburned forest, size, and severity of the burn) would have the most impact on occupancy of nest cavities. Site characterized spatial scale, which had a greater influence on occupancy by strong than weak excavators. We know that selection of habitat scale varies by species, although we do not fully understand the mechanisms that underlie these differences. Availability of insect prey likely had an important influence on the scale of habitat used by the two groups of excavators that differed in their foraging strategies. The group of strong excavators was dominated by wood- and ground-foraging species (Hairy Woodpecker and Northern Flicker), whereas the weak excavator (Lewis's Woodpecker) foraged primarily on flying arthropods.

TIME AND SITE EFFECTS ON OCCUPANCY

Whether time since fire was constrained into two time periods (years 1–4 and 5–7 postfire) or used in the full time model, it was the best pre-

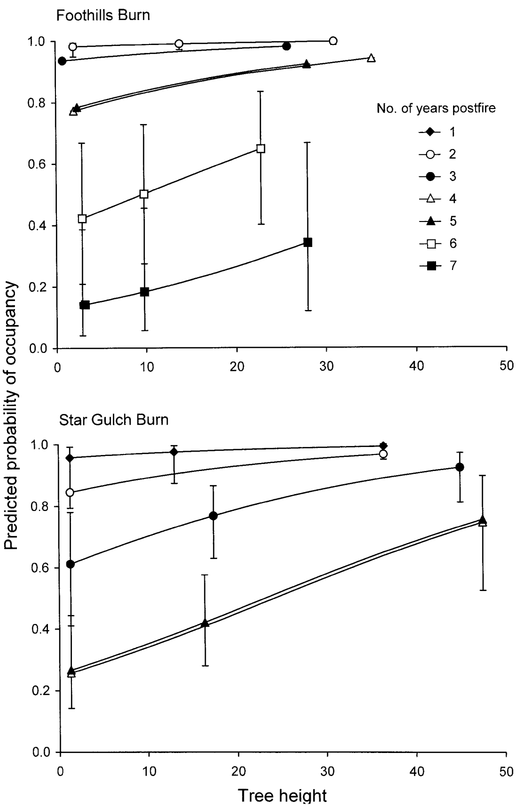

FIGURE 2. Predicted probabilities of cavity occupancy for strong excavators based on tree heights, derived from logistic regression model results. Predicted probabilities represent $n = 404$ trials in the Foothills Burn and $n = 171$ trials in the Star Gulch Burn for nest cavities oriented in an easterly direction, in trees with decay class 2. Error bars represent the 95% confidence intervals for estimates associated with the minimum, median, and maximum values observed for tree height.

dictor of cavity occupancy. Odds of occupancy were greater in the early period and lower in the later period. The time periods were selected because of expected biological and physical changes by four to five years after fire. Forest structure, insect assemblages, and vertebrate communities change rapidly in these early postfire years (e.g., Blackford 1955, Raphael et al. 1987). Rates of change generally depend on burn severity, and pre- and postfire vegetation (Huff and Smith 2000, Saab et al. 2002, Kotliar et al. 2002). Snag decay and falling rates increase (Morrison and Raphael 1993, Bull et al. 1997), numbers of bark and wood-boring beetles decline significantly (e.g., McCullough et al.

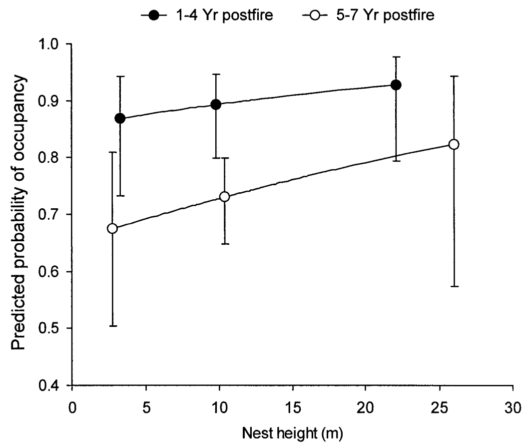

FIGURE 3. Predicted probabilities of cavity occupancy for weak excavators based on nest height, derived from logistic regression model results. Predicted probabilities represent $n = 75$ trials for years 1–4 postfire and $n = 131$ trials for years 5–7 postfire. Error bars represent the 95% confidence intervals for estimates associated with the minimum, median, and maximum values observed for nest height.

1998), and mammalian and reptilian nest predators begin to recolonize, as suggested by Saab and Vierling (2001). At the same time, shrub development and associated arthropods increase with year postfire (e.g., Bock 1970, Lowe et al. 1978, Huff et al. 1985). Such changes during the early postfire years evidently affect occupancy

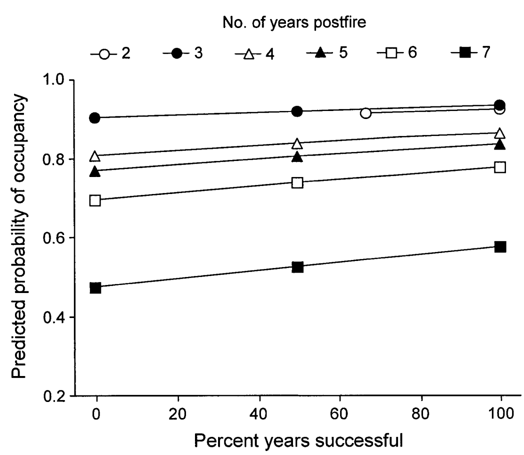

FIGURE 4. Predicted probabilities of occupancy for weak excavators based on the percentage of years an occupied cavity was successful, derived from logistic regression model results. Predicted probabilities represent $n = 13$, $n = 28$, $n = 34$, $n = 60$, $n = 39$, and $n = 32$ trials for years 2 through 7 postfire, respectively.

TABLE 6. Parameter estimates ± SE, and adjusted odds ratios from the five best models (Table 4) for predicting probability of occupancy of nest cavities by weak excavators (Lewis's Woodpecker) in recently burned forests of southwestern Idaho during 1994–1999. Odds ratios for categorical variables indicate the odds of occupancy for one category level relative to another category level (specified in ''contrast'' column). Odds ratios for continuous variables indicate the odds of occupancy for every 1-unit change in the variable. Confidence limits that do not contain 1 are considered statistically significant.

Model Parameter Value	Parameter estimate ± SE	Adjusted odds ratio		
		Contrast	Estimate	Confidence limits
Model 1				
Intercept	1.57 ± 0.21			
Postfire period				
Early	0.56 ± 0.21	Early vs. late	3.1	1.4–7.5
Model 2				
Intercept	1.60 ± 0.25			
Year postfire				
2	0.88 ± 0.88	2 vs. 4	2.1	0.3–41.8
3	0.96 ± 0.65	3 vs. 4	2.2	0.4–16.6
5	–0.11 ± 0.37	5 vs. 4	0.8	0.2–2.3
6	–0.54 ± 0.39	6 vs. 4	0.5	0.1–1.6
7	–1.35 ± 0.38	7 vs. 4	0.2	0.06–0.7
Model 3				
Intercept	1.20 ± 0.45			
Postfire period				
1	0.57 ± 0.21	1 vs. 2	3.1	1.4–7.7
Nest height	0.04 ± 0.04		1.0	1.0–1.1
Model 4				
Intercept	1.28 ± 0.44			
Year postfire				
2	0.82 ± 0.89	2 vs. 4	1.9	0.3–39.2
3	0.95 ± 0.65	3 vs. 4	2.2	0.4–16.3
5	–0.07 ± 0.37	5 vs. 4	0.8	0.2–2.4
6	–0.45 ± 0.40	6 vs. 4	0.5	0.2–1.8
7	–1.39 ± 0.39	7 vs. 4	0.2	0.06–0.7
Years successful	0.41 ± 0.46		1.5	0.6–3.7
Model 5				
Intercept	1.55 ± 0.23			
Postfire period				
1	0.56 ± 0.21	1 vs. 2	3.1	1.4–7.5
Site				
Foothills	0.03 ± 0.21	Foothills vs. Star Gulch	1.1	0.5–2.3

of nest cavities (this study), reproductive success (Saab and Vierling 2001), and foraging habitat (Murphy and Lehnhausen 1998) of cavity-nesting birds.

Probability of cavity occupancy by strong excavators declined by the fourth year postfire in the Star Gulch Burn and by the sixth year postfire in the Foothills Burn, even when decay and orientation remained constant (Fig. 2). This decline was particularly evident in the Star Gulch Burn. Apparently, other factors affected occupancy of nest cavities in these later postfire years, perhaps including inherent characteristics of site, nest predation, food availability, or competition for cavities.

Nest-site competition was an unlikely explanation of declines in cavity occupancy based on the low rates of cavity reuse in our study area. In addition to reuse patterns, nesting densities of Lewis's Woodpecker were used as a proxy for nest-site competition because this species usurps nests of other cavity nesting species (Tobalske 1997; Saab and Dudley, unpubl. data). However, cavity occupancy declined sooner in the study at the Star Gulch Burn than at the Foothills Burn. Because the Star Gulch Burn had lower nesting densities of Lewis's Woodpecker than the Foothills Burn, we regard nest usurpation by Lewis's Woodpecker as a poor explanation for declines in cavity occupancy.

Higher snag densities in the Star Gulch Burn presumably provided greater foraging opportunities for bark- and wood-foraging woodpeckers (Saab et al. 2002), assuming that food availability was limited by snag numbers. Yet declines in occupancy were more rapid in the unlogged Star Gulch Burn than in the logged Foothills Burn. Although the predicted declines in cavity occupancy occurred in different postfire years at the two burn sites, the declines occurred in the same calendar years, 1998–1999. This possibly suggests an actual year effect that could have influenced food availability or nest predators.

In combination with time and space effects, tree and nest height affected the predicted probabilities of cavity occupancy by strong and weak excavators, respectively. Tree and nest heights were not only important in predicting cavity occupancy but their values changed through time. Because strong excavators readily create nest cavities, their selection for various tree heights was expected. In contrast, selection for nest height rather than tree height was expected for Lewis's Woodpecker because it has a weaker ability to excavate its own nest cavities and more commonly selects nests from existing cavities (Table 2; Fig. 1). Nest occupancy by strong excavators was consistently high for all tree heights during the early postfire years. In the later years, however, the probability of occupancy was lower for cavities in shorter trees but increased with tree height (Fig. 2). Tree height was positively correlated with nest height for cavities occupied by strong excavators in our study areas ($r = 0.67$, $P < 0.001$). Perhaps strong excavators selected taller trees (and correspondingly higher nests) to reduce the risk of nest predation in the later postfire years (4–7), a period in which nest predators may have had time to recolonize the burns.

Similarly, we observed that probability of occupancy by weak excavators (Lewis's Woodpecker) was consistently high at all nest heights in the early postfire years. In the later postfire years, however, the probability of occupancy was lower for lower nest cavities but increased with nest height. Nest predators could have been responsible for the observed changes in cavity occupancy because they strongly influence the use and success of nest cavities (Nilsson 1984, Li and Martin 1991). The patterns in occupancy of nest cavities that we observed in burned forests were similar to patterns observed in nest success of cavity-nesting birds in green forests. Lower nest success was reported for individuals and species with lower nest heights, where predation was the main cause of nest failure (Nilsson 1984, 1986, Rendell and Robertson 1989, Li and Martin 1991, Albano 1992).

We propose that nest predation underlies the observed effects of time since fire and cavity height on occupancy. Fire reduces numbers of small mammalian and reptilian nest predators. They begin to recolonize by the fourth year after fire, and the rate of recolonization depends on the patchiness of the burn. As nest predators recolonize the burns, predation pressure increases and consequently, cavity nesters use less predator-accessible cavities. Small mammalian and reptilian nest predators commonly observed in or near our study area include red squirrels (*Tamiasciurus hudsonicus*), weasels (*Mustela* spp.), and bullsnakes (*Pituophis melanoleucus*).

The Star Gulch Burn was relatively small, characterized by mixed fire severities, and a mosaic of unburned forest, whereas the Foothills Burn was larger, created by more high-severity fire, with little unburned forest remaining after the fire. Close proximity and interspersion of unburned forest patches potentially provided greater access for nest predators into the Star Gulch Burn. Nest predators likely had time and access to recolonize the burn by the fourth year after fire, increasing predation pressures and decreasing occupancy of nest cavities in the Star Gulch Burn. Declines in predicted probability of occupancy in the larger and presumably less predator-accessible Foothills Burn were not evident until the sixth year after fire. The mean percentage of nesting attempts that failed due to predation varied little between the two burned sites during the period in which we monitored nest success of all species (1994–1997; Foothills mean 19.0 ± 2.2%, $n = 4$ years; Star Gulch mean 17.7 ± 2.5%, $n = 3$ years; Saab and Dudley, unpubl. data). Numbers of nest predators and causes of nest failures should be studied concurrently during early postfire years to test our hypothesis that nest predation is the mechanism responsible for changes in cavity occupancy.

EFFECTS OF CAVITY REUSE PATTERNS ON OCCUPANCY

Occupancy by strong excavators was not explained by models with parameters that characterized reuse patterns: number of species using a cavity, percent reused by the same guild, and percent of years with a successful nest. This result was anticipated for strong excavators in our study area because they rarely (2% of nests) reused nest cavities.

Percentage of years with a successful nest, however, was important for predicting cavity occupancy by Lewis's Woodpecker, our only weak excavator. Once a Lewis's Woodpecker occupied a nest cavity, it apparently maintained occupancy over several years. Reuse of cavities by this woodpecker was nearly 50%, the highest among the species that we studied. This pattern was not surprising based on their aggressive nature and ability to usurp nests of other cavity nesters, and their weak excavator morphology (Tobalske 1997; Saab and Dudley, unpubl. data). Assuming that risk of predation increases over time after fire, the percentage of years with a successful nest should have a stronger influence in the later postfire years. Indeed, this was the pattern that we observed and it was particularly important in postfire year 7.

Nest tree species was unimportant for cavity occupancy or reuse in our study area. Ponderosa pine was the most frequently used tree for nesting but it was also the most abundant tree species; thus no selection for tree species was evident. Tree species selection was important for reuse of cavities in unburned forests of British Columbia (Aitken et al. 2002). Cavity nesters favored quaking aspen for both cavity excavation and reuse. Opportunities and actual nesting use of aspen were rare in our study area (Appendix), perhaps because it was uncommon and patchily distributed. When aspen is available, it plays a key role in the nesting ecology of cavity-nesting birds (Dobkin et al. 1995, Aitken et al. 2002, Martin et al. 2004).

MICROHABITAT EFFECTS ON OCCUPANCY

Snags were abundant in postfire years 1 and 2, but not easily excavated because trees had little time to decay (Hutto 1995, Saab and Dudley 1998). Broken-topped or forked trees were typical characteristics of decay class 2, which were the trees most commonly excavated and most likely to have occupied cavities based on our models. This pattern was not surprising because tree decay varied little throughout the study period (Appendix), and only 1 of 385 trees had a change in decay class during our study, from class 2 to class 3.

Cavity orientation in an easterly direction was another nest tree characteristic included in the best model for predicting cavity occupancy by strong excavators. Several factors may have influenced cavity occupancy in this direction, including weather, thermal environment, and heartrot (Conner 1975, Daily 1993). In western Idaho, prevailing winds blow from the southwest, which may have deterred occupancy of cavities facing that direction. An easterly direction may have aided in warming the cavity during the morning hours, the period with the lowest daytime temperatures. If heartrot were more prevalent on the east side of trees, this would have provided opportunities for excavation.

Unlike strong excavators, occupancy by Lewis's Woodpecker was not explained by models with parameters that characterized nest tree features, such as decay and orientation. Such results were unsurprising because strong excavators have a greater physical ability to select the placement of their cavities in relation to tree decay and entrance orientation. Species with weak excavator morphology (i.e., Lewis's Woodpecker) are limited by their physical ability to excavate, resulting in less control over the placement of their cavities.

Models with other parameters that described nest trees (diameter and snag density surrounding nest trees) did not explain cavity occupancy. Studies comparing nest cavity use to availability reported that tree diameter and density were important for nest-site selection by cavity-nesting birds (Raphael and White 1984, Li and Martin 1991, Saab et al. 2002). In this study, however, we compared cavity occupancy to vacancy of selected nest trees that were used for nesting in one or more years of our study. Our results, therefore, could not be expected to follow the same pattern.

We did not measure cavity entrance size and volume, although these factors are reported to be important for cavity reuse because they influence the species that can use cavities (Peterson and Gauthier 1985, Aitken et al. 2002). In these studies there was a large variance in the size of birds that were using nest cavities (e.g., from Tree Swallows [*Tachycineta bicolor*] to Buffleheads [*Bucephala albeola*]), thus size and volume of the cavity was expected to be important. In our study, body size was not highly variable among the common nesting species (i.e., Mountain Bluebirds to Northern Flickers). Based on visual estimations of cavity entrance shape and size, Hairy Woodpeckers and Northern Flickers were responsible for creating nearly 70% of the cavities in our study area (Appendix). Consequently, cavity entrance size and volume probably varied little and were likely not important features for determining occupancy by cavity-nesting species, with the exception of American Kestrel (an uncommon nesting species; Table 1).

Understanding the temporal changes in habitats and populations is essential for the conservation and management of cavity-nesting birds using recently burned forests (Hutto 1995, Martin and Eadie 1999, Saab and Vierling 2001). Habitat created by fire is an ephemeral resource. Our study suggests the need for replacing this ephemeral resource to maintain suitable breeding habitat for cavity-nesting birds. Results from our research help in understanding how long cavity-nesting birds persist in burned habitats. Additionally, we have documented that the length of time in which recently burned forests remain suitable habitat varies by site, depending on size, severity, and mosaic of the burn. We still do not know what portion of the landscape or how long these ephemeral habitats are needed to sustain populations of cavity-nesting birds across western North American forests.

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LITERATURE CITED

AITKEN, K. E. H., K. L. WIEBE, AND K. MARTIN. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119: 391–402.

ALBANO, D. J. 1992. Nesting mortality of Carolina Chickadees breeding in natural cavities. Condor 94:371–382.

ALLISON, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Inc., Cary, NC.

ANDERSON, D. R., W. A. LINK, D. H. JOHNSON, AND K. P. BURNHAM. 2001. Suggestions for presenting the results of data analyses. Journal of Wildlife Management 65:373–378.

APFELBAUM, S., AND A. HANEY. 1981. Bird populations before and after wildfire in a Great Lakes pine forest. Condor 83:347–354.

BEST, L. B. 1979. Effects of fire on a Field Sparrow population. American Midland Naturalist 101: 434–442.

BLACKFORD, J. L. 1955. Woodpecker concentration in burned forest. Condor 57:28–30.

BOCK, C. E. 1970. The ecology and behavior of the Lewis Woodpecker. University of California Publications in Zoology 92:1–100.

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.

BOCK, C. E., M. RAPHAEL, AND J. H. BOCK. 1978. Changing avian community structure during early post-fire succession in the Sierra Nevada. Wilson Bulletin 90:119–123.

BULL, E. L., C. G. PARKS, AND T. R. TORGERSEN. 1997. Trees and logs important to wildlife in the Interior Columbia River Basin. USDA Forest Service General Technical Report PNW-GTR-391.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

CLINE, S. P., A. B. BERG, AND H. W. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:773–786.

CONNER, R. N. 1975. Orientation of entrances to woodpecker nest cavities. Auk 92:371–374.

DAILY, G. C. 1993. Heartwood decay and vertical distribution of Red-naped Sapsucker nest cavities. Wilson Bulletin 105:674–679.

DIXON, R. D., AND V. A. SAAB. 2000. Black-backed Woodpecker (*Picoides arcticus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 509. The Birds of North America, Inc., Philadelphia, PA.

DOBKIN, D. S., A. C. RICH, J. A. PRETARE, AND W. H. PYLE. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. Condor 97:694–707.

DUDLEY, J., AND V. SAAB. 2003. A field protocol to monitor cavity-nesting birds. USDA Forest Service Research Paper RMRS-RP-44.

ESRI. 1999. ArcView GIS 3.2. Environmental Systems Research Institute, Inc., Redlands, CA.

HORST, G. A. 1970. The effects of controlled burning on arthropod density and biomass in relation to bobwhite quail brood habitat on a right-of-way. Tall Timbers Conference on Ecological Animal Control by Habitat Management 2:173–183.

HOSMER, D. W., AND S. LEMESHOW. 2000. Applied logistic regression. 2nd ed. Wiley, New York.

HUFF, M. H., J. K. AGEE, AND D. A. MANUWAL. 1985. Postfire succession of avifauna in the Olympic Mountains, Washington, p. 8–15. *In* J. E. Lotan and J. K. Brown [COMPILERS], Fire's effects on wildlife habitat-symposium proceedings, Missoula, MT. USDA Forest Service General Technical Report INT-GTR-186.

HUFF, M. H., AND J. K. SMITH. 2000. Fire effects on animal communities, p. 35–42. *In* J. K. Smith [ED.], Wildland fire in ecosystems: effects of fire on fauna. Vol. 1. USDA Forest Service General Technical Report RMRS-GTR-42.

HURVICH, C. M., AND C. TSAI. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9:1041–1058.

KOTLIAR, N. B., S. HEJL, R. L. HUTTO, V. SAAB, C. P. MELCHER, AND M. E. MCFADZEN. 2002. Effects of wildfire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25:49–64.

LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

LINDER, K. A., AND S. H. ANDERSON. 1998. Nesting habitat of Lewis' Woodpeckers in southeastern Wyoming. Journal of Field Ornithology 69:109–116.

LOWE, P. O., P. F. FOLLIOTT, J. H. DIETERICH, AND D. R. PATTON. 1978. Determining potential wildlife benefits from wildfire in Arizona ponderosa pine forests. USDA Forest Service General Technical Report RM-GTR-52.

MANY, D. E. 1984. Factors influencing the use of winter-burnt grassland by foraging Bald Ibises (*Geronticus calvus*). South African Journal of Zoology 19:12–15.

MARTIN, K., K. E. H. AITKEN, AND K. L. WIEBE. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. Condor 106:5–19.

MARTIN, K., AND J. M. EADIE. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115:243–257.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. 2nd ed. Chapman and Hall, New York.

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.

MORRISON, M. L., AND M. G. RAPHAEL. 1993. Modeling the dynamics of snags. Ecological Applications 3:322–330.

MURPHY, E. C., AND W. A. LEHNHAUSEN. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62:1359–1372.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15:167–175.

NILSSON, S. G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103: 432–435.

PETERSON, B., AND G. GAUTHIER. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. Wilson Bulletin 97:319–331.

RAPHAEL, M. G., M. L. MORRISON, AND M. P. YODER-WILLIAMS. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. Condor 89:614–626.

RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

RENDELL, W. B., AND R. J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for Tree Swallows breeding in natural cavities. Condor 91:875–885.

SAAB, V., R. BRANNON, J. DUDLEY, L. DONOHOO, D. VANDERZANDEN, V. JOHNSON, AND H. LACHOWSKI. 2002. Selection of fire-created snags at two spatial scales by cavity-nesting birds, p. 835–848. *In* P. J. Shea, W. F. Laudenslayer Jr., B. Valentine, C. P. Weatherspoon, and T. E. Lisle [EDS.], Proceedings of the symposium on the ecology and management of dead wood in western forests, November 2–4, 1999, Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-181.

SAAB, V. A., AND J. G. DUDLEY. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. USDA Forest Service Research Paper RMRS-RP-11.

SAAB, V. A., AND K. VIERLING. 2001. Reproductive success of Lewis's Woodpecker in burned pine and cottonwood riparian forests. Condor 103:491–501.

SAS INSTITUTE. 2000. SAS/STAT user's guide. Vol. 2. Version 8. SAS Institute, Inc., Cary, NC.

TOBALSKE, B. W. 1997. Lewis' Woodpecker (*Melanerpes lewis*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 284. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

YOCCOZ, N. G. 1991. Use, overuse, and misuse of significance tests in evolutionary biology and ecology. Bulletin of the Ecological Society of America 72:106–111.

APPENDIX. Summary statistics (mean ± SE except where noted) for the covariates used in modeling occupancy of nest cavities and other descriptive variables for the study area. Sample sizes are reported in Table 1; Table 2 lists strong and weak excavators; Table 3 defines covariates.

Variable	Foothills Burn	Star Gulch Burn	Study area
Covariates used in models			
Decay (class)	2.0 ± 0.05	2.0 ± 0.04	2.0 ± 0.03
Diameter at breast height (cm)	45.2 ± 1.4	47.9 ± 1.4	46.6 ± 1.0
Cavity height (m)	8.5 ± 0.4	10.0 ± 0.4	9.3 ± 0.3
Tree height (m)	15.3 ± 0.6	18.0 ± 0.7	16.7 ± 0.5
Number of species	1.2 ± 0.4	1.1 ± 0.02	1.2 ± 0.02
Snag density (*n* per 0.04 ha)	8.1 ± 0.5	11.1 ± 0.4	9.7 ± 0.3
Orientation (frequency; *n* cavities)			
0–60°	29	36	65
61–120°	31	34	65
121–180°	43	39	82
181–240°	17	33	50
241–300°	22	25	47
301–359°	38	38	76
Precipitation (mm)			
1994			23.2 ± 10.5
1995			60.8 ± 17.1
1996			45.7 ± 14.6
1997			37.7 ± 3.9
1998			54.7 ± 27.6
1999			16.2 ± 5.9
Same guild (%)	90 ± 0.02	94 ± 0.01	92 ± 0.01
Site			
Landscape context (% unburned)	0.04 ± 0.002	0.15 ± 0.005	0.10 ± 0.004
Potential nest competition (no. of Lewis's Woodpecker nests within 300 m)	6.5 ± 0.4	4.7 ± 0.4	5.4 ± 0.3
Years successful (%)	78 ± 3	85 ± 2	82 ± 2
Other descriptive variables			
Original excavator (% of all cavities)			
Strong	77	90	84
Weak	23	10	16
Nest tree species (% frequency)			
Ponderosa pine	69	54	61
Douglas-fir	29	38	34
Quaking aspen	1	8	5
Subalpine fir	0	1	<1
Scouler's willow	1	0	<1