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RED-HEADED WOODPECKER NEST-SITE SELECTION AND REPRODUCTION IN MIXED PONDEROSA PINE AND ASPEN WOODLAND FOLLOWING FIRE

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Abstract. Red-headed Woodpecker (*Melanerpes erythrocephalus*) populations are declining at a continental scale, yet little is known about their nest-site selection and reproduction within burned forests. We measured reproductive parameters and nest-site characteristics at 17 Red-headed Woodpecker nests and 17 random sites between 2001 and 2004 in the Black Hills, South Dakota. The average date the first egg was laid was 17 June, and the average clutch size was 5.4 ± 0.4. The daily nest survival rate averaged 0.98 (overall nest success = 47%), and predation was the major cause of nest failure. Red-headed Woodpecker nests occurred farther from grassland edges in large diameter snags within severely burned quaking aspen (*Populus tremuloides*) stands. High-severity fire within these aspen stands resulted in a combination of snag and understory characteristics that differed from the surrounding pine forest matrix. Interactions between cover type and burn severity may have important ecological consequences for Red-headed Woodpeckers in a mixed conifer forest.

Key words: aspen, Black Hills, burn severity, habitat selection, Melanerpes erythrocephalus, Populus tremuloides, *Red-headed Woodpecker.*

Selección de Sitios de Nidificación y Reproducción de *Melanerpes erythrocephalus* en Bosques Mixtos de Pino Ponderosa y Álamo luego de ser Incendiados

Resumen. Las poblaciones de *Melanerpes erythrocephalus* están disminuyendo a escala continental y sin embargo se conoce poco sobre la selección de sitios de nidificación y la reproducción de esta especie en bosques incendiados. Medimos parámetros reproductivos y características de los sitios de nidificación en 17 nidos de *M. erythrocephalus* y en 17 sitios aleatorios entre los años 2001 y 2004 en Black Hills, Dakota del Sur. La fecha promedio en que fue puesto el primer huevo fue el 17 de junio y el tamaño promedio de la nidada fue de 5.4 ± 0.4. La tasa diaria de supervivencia del nido promedió 0.98 (éxito global del nido = 47%), y la depredación fue la principal causa de fracaso del nido. Los nidos de *M. erythrocephalus* se ubicaron alejados de los bordes con los pastizales, en árboles muertos en pie de gran diámetro, dentro de bosques severamente quemados de *Populus tremuloides*. La incidencia de fuegos muy severos al interior de estos bosques de álamo generó una combinación de características de los árboles muertos en pie y del sotobosque que difirieron de la matriz periférica de bosque de pino. Las interacciones entre el tipo de cobertura y la severidad del incendio pueden tener consecuencias ecológicas importantes para *M. erythrocephalus* en los boques mixtos de coníferas.

Red-headed Woodpeckers (*Melanerpes erythrocephalus*) occupy both deciduous and coniferous forests from eastern North America to the Midwest, and have been experiencing population declines across their range (Smith et al. 2000, Sauer et al. 2005). Historical accounts suggest that this species was once common in the Black Hills of South Dakota: Grinnell (1875) described Red-headed Woodpeckers as "especially abundant," and Cary (1901) noted that it was "the most abundant woodpecker in the hills." As with many western forests, the Black Hills are actively managed, and Sauer et al. (2005) have noted

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declines of this species in the Black Hills. Smith et al. (2000) suggested that general threats to this species include loss of snags and associated foraging habitat. Red-headed Woodpeckers are aerial flycatchers and a relatively open, productive understory surrounding nest sites is likely necessary to provide foraging opportunities for this species (Wilson et al. 1995). Removal of snags may limit nesting opportunities because Red-headed Woodpeckers rely heavily on large snags for nesting (Gutzwiller and Anderson 1987).

Red-headed Woodpeckers have been recorded in burned forests (Niemi 1978, Stevenson and Anderson 1994), but the relative use by and importance of burned forests to Red-headed Woodpeckers is unknown. Fire can create snags for nesting and productive understories that can support high arthropod densities (Turner et al. 1994, Lentile 2004). Wilson et al. (1995) found that prescribed burns and understory clearing increased Red-headed Woodpecker densities, presumably because the combination of activities produced a suitable balance of snags and open flycatching habitat. However, fires can also destroy existing snags used for nesting, so the effects of fire on potential breeding habitat for Red-headed Woodpeckers may be mixed depending on site-specific fire and forest management history.

Over the last century, fire frequencies and average fire intensities in pine forests have changed across North America (Covington and Moore 1994), and fire suppression has led to less diverse and more continuous vegetation communities in landscapes that were once more patchy. With increasing occurrence of stand-replacing fires in western pine forests, it becomes important to understand patterns of use and reproduction in these habitats by species such as Red-headed Woodpeckers. To our knowledge, no studies have addressed nest-site selection and reproduction of Red-headed Woodpeckers in burned forests, and few studies have addressed Red-headed Woodpecker nest-site selection and reproduction in the western portions of their range. Therefore, our primary objective was to examine Red-headed Woodpecker nest-site selection and reproduction in a mixed-severity burn in the Black Hills, South Dakota.

METHODS

STUDY SITES

The Black Hills are an isolated and forested mountain range rising over 1000 m above the Great Plains of western South Dakota and northeastern Wyoming (Shepperd and Battaglia 2002). The Black Hills are dominated by ponderosa pine (*Pinus ponderosa*), but include patches of aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), bur oak (*Quercus macrocarpa*), and white spruce (*Picea glauca*; Shinneman and Baker 1997). The historical disturbance regime of ponderosa pine forests in the Black Hills is diverse. The southern portion of the Black Hills is arid and dominated by shortgrass prairie and homogeneous ponderosa pine forests. Dendrochronologically based studies from the southern Black Hills suggest that low intensity surface fires burned every 10–30 years (Brown and Sieg 1996). These fires reduced understory growth and maintained open savannah-like forests with relatively large trees. The northern Black Hills are wetter and cooler than the southern region and stand-replacing fires occurred approximately every 70 years (Shinneman and Baker 1997). Current forest structure has been influenced by both large, stand-replacing crown fires and small, less severe surface disturbances. Thus, contemporary Black Hills fire regimes may be best described as mixed-severity (Lentile 2004).

In late August and early September 2000, the Jasper fire burned 33 795 ha of interior forests in the southern Black Hills. This fire burned under very low fuel moisture and high wind conditions (Benson and Murphy 2003), and was ~25% larger than any other recorded fire in Black Hills history (USDA Forest Service 2001). The burned area was located between 43°41′ and 43°55′N and 103°46′ and 104°0′W, and at elevations of ~1500–2100 m. The Jasper fire was started by arson (Shepperd and Battaglia 2002) in an area that had not burned in the previous century (Brown and Sieg 1996).

Saab et al. (2002) noted that prefire canopy cover was a good predictor of occupancy by woodpeckers, specifically Black-backed Woodpeckers. Prefire canopy cover might also be important in examining postfire use by other woodpecker species, including Red-headed Woodpeckers, who are known to select for relatively open woodlands (Smith et al. 2000). Thus, within the Jasper fire region, we established six study sites of 300–400 ha with varying prefire forest canopy cover. Two of the study sites were dominated by "high" (>70%) prefire canopy cover, two of the study sites were dominated by "medium" (40%–70%) prefire canopy cover, and two of the study sites were dominated by "low" (<40%) prefire canopy cover (Saab et al. 2002).

FIELD METHODS

Nest searching to document woodpecker nesting activity occurred for four years, beginning the first spring following the fire. We followed nest searching methods described in Dudley and Saab (2003) to find Red-headed Woodpecker cavities. We established transects every 200 m within each study site, and searched for nests by walking each transect until the entire unit had been surveyed (Dudley and Saab 2003). We conducted nest surveys from late April through early July each year. Once found, we monitored nests every 3–4 days with a TreeTop cavity viewer (Sandpiper Technologies, Inc., Manteca, California) until they failed or young fledged. To determine the first day an egg was laid ("first egg date"), we assumed that durations of Red-headed Woodpecker nesting stages were similar to those elsewhere in their range. Smith et al. (2000) summarized the number of days required for incubation and fledging, and we used these figures for our calculations (12 days for incubation, 27 days for the nestling phase). Daily survival rates were determined using Shaffer (2004), and causes of nest failure were recorded for all nests where possible.

We recorded cavity and microhabitat characteristics following BBIRD protocol (Martin et al. 1997) for 17 nest sites and 17 random sites. Random sites were centered on a random tree. Random trees were selected by using a random number generator to determine coordinates for random sites. These random sites were a minimum of 50 m from the nest tree, and were in the same cover type and study sites as nest trees. At nest trees, we waited until the nest had failed or young had fledged before making measurements. We recorded tree and cavity height, cavity age, snag species, decay class, and diameter at breast height (dbh). Microsite characteristics included cover type (either aspen or pine), shrub density, and snag density. Within a 5 m radius of the nest or random tree, we recorded the number of shrub stems <2.5 cm dbh, 2.5–5.0 cm dbh, and 5–8 cm dbh. We also recorded of the number of snags >23 cm dbh within 11.3 m of the nest or random tree (0.04 ha; Martin et al. 1997).

In addition, we examined habitat selection in the context of burn severity, since severity might influence both snag abundance and food availability. We used GIS-based burn severity data generated by the Black Hills National Forest to classify nest and random sites. Burn severity classes ranged from low (surface fire) to moderate (mixed surface fire and torching) to high (stand-replacing fire). Low-severity burn areas had low tree mortality, predominantly green tree canopies (<25% canopy scorch), and >70% vegetated ground cover. Moderate-severity burns had mixed tree mortality and survival, extensively scorched tree canopies (>25% scorch), and 30%–70% vegetated ground cover. High-severity fires were characterized by complete tree mortality (100% blackened canopies) and less than 30% vegetated ground cover (Lentile 2004). We used the Spatial Analyst© extension in ArcView GIS® (ESRI, Redlands, California) to calculate minimum distances from each nest or random site to nonforested edges (distance to edge). Additionally, we created 1 km radius buffers around each nest or random site to examine the percentage of low, moderate, and high severity fire within a 1 km radius.

STATISTICAL ANALYSES

We modeled Red-headed Woodpecker habitat selection using PROC LOGISTIC in SAS 9.01 (SAS Institute 2001), and we used an information-theoretic approach (Burnham and Anderson 2002) to determine the best model among an *a priori* set consisting of a fully parameterized global model and its reduced forms. We applied the Hosmer-Lemeshow goodness-of-fit test to the global model to ensure that it adequately fit the data (Hosmer and Lemeshow 2000). We then determined the overdispersion parameter ($\hat{c}$; Pearson's χ^2 divided by the degrees of freedom) to assess whether a quasi-likelihood correction was necessary (Burnham and Anderson 2002).

We selected among candidate models using Akaike's information criterion corrected for small sample sizes (AIC_c). The ΔAIC_c score is the difference between the model with the lowest AIC_c score and each other candidate model. In general, a ΔAIC_c score between 0 and 2 suggests substantial support for the model, a ΔAIC_c between 4 and 7 represents much less support for the model, and a ΔAIC_c of greater than 10 represents essentially no support for the model (Burnham and Anderson 2002).

We examined habitat selection in relation to five covariates: dbh of the cavity tree, density of shrubs within a 5 m radius of the nest tree, density of snags >23 cm within 0.04 ha of the focal tree, distance (m) to nonforested edge, and the percentage of high-severity fire within a 1 km radius surrounding the focal tree. In general, these variables were chosen because they have been reported as important determinants of nest-site selection for Red-headed Woodpeckers in other regions (Smith et al. 2000), or they have been noted to be important determinants of nest-site selection for the closely related Lewis's Woodpecker (*Melanerpes lewis*; Vierling 1997), which is similar ecologically to the Red-headed Woodpecker. To our knowledge, no studies have examined the influence of burn severity on habitat selection of Red-headed Woodpeckers, although it may be important due to its influence on foraging habitat and snag availability.

We compared 25 candidate models to examine habitat selection. We used PROC LOGISTIC to calculate the adjusted odds ratios and 95% confidence intervals for parameters of interest as indicated by the model with the lowest AIC_c score. We did not use a quasi-likelihood correction factor for the AIC_c rankings because the overdispersion parameter was <1. All values are presented as means ± SE, and a $P < 0.05$ is considered statistically significant.

RESULTS

Before the Jasper fire, the study sites were dominated by ponderosa pine (~88%) with aspen stands comprising ~2% of the landscape. Burn severities differed within these cover types. Eighteen percent of ponderosa pine forests burned at low severity, 53% burned at moderate severity, and 29% burned at high severity. Low burn severity was most common in aspen stands (55%), with 24% burned at moderate severity, and 21% burned at high severity.

Nest-site selection analyses were based on 17 nests found between 2001 and 2004, while analyses of reproductive parameters were based on 17 nesting attempts (including two renests) that occurred between 2002 and 2004; nesting data from 2001 were not included because we lacked a cavity viewer and did not visit nests consistently that year. Red-headed Woodpeckers had first egg dates that ranged from 28 May to 2 July ($n = 7$) with an average first egg date of 17 June. Clutch sizes averaged 5.4 ± 0.4 and the daily survival rate was 0.98 (approximately 47% overall nest success). Predation accounted for 78% of nest failures.

All nests were in snags and, while severely burned aspen stands represented a very small fraction of the landscape, 53% of nests (9 of 17) occurred in aspen snags within these aspen stands. The remaining nests all occurred in ponderosa pine. In general, tree dbh, shrub density, distance to edge, and the percentage of high-severity fire within 1 km of the nest tree were all higher at nest sites than random sites (Table 1).

TABLE 1. Summary statistics (mean ± SE) for the covariates used in modeling Red-headed Woodpecker nest-site selection in the Black Hills, South Dakota, 2001–2004 and other descriptive variables. Covariates in the models included DBH (cm) for nest and random trees, the density of shrub stems <2.5 cm DBH within 0.04 ha of the nest and random trees, the number of snags and trees >23 cm DBH recorded in 11.3 m radius plots (0.04 ha) centered at each nest and random tree, the distance (m) to the nearest patch of grassland, and the percent of area within a 1 km radius burned by high-severity fire. Also included are additional descriptive data on tree height (m) and decay class following Cline et al. (1980), where 0 = live and 5 = most decayed.

Habitat variable	Nest sites	Random sites
DBH (cm)	27.4 ± 1.3	20.5 ± 2.6
Shrub density	89.4 ± 28.3	32.2 ± 13.0
Snag density	2.9 ± 0.5	3.3 ± 0.8
Distance to edge (m)	456.9 ± 66.0	317.6 ± 60.8
% high severity	40.6 ± 4.5	31.5 ± 3.3
Tree height (m)	14.1 ± 1.1	12.9 ± 1.5
Decay class	2.1 ± 0.2	1.9 ± 0.3

Goodness-of-fit tests indicated that the global model for habitat selection adequately fit the data ($P = 0.92$). Of the 25 models that we assessed, only one model received substantial support (i.e., had a ΔAIC_c of <2). This model contained the covariates dbh, distance to edge, and percent high severity burn within 1 km of the nest site (Table 2). All other models had a ΔAIC_c of at least 3.4. Parameter estimates from the best model indicated that nest sites were positively associated with larger nest trees ($\hat{\beta} = 0.26 \pm 0.09$), higher percentages of high-severity fire within the 1 km buffer ($\hat{\beta} = 0.14 \pm 0.06$), and greater distances from forest-grassland edges ($\hat{\beta} = 0.01 \pm 0.00$).

DISCUSSION

Reproductive parameters for Red-headed Woodpeckers have not been reported from burned habitats or sites within the Black Hills. Average first egg date, though based on a small sample size, lies within the range of dates summarized by Smith et al. (2000). Daily survival rates in this stand-replacing burn were low compared to previous studies. Reported nesting success for Red-headed Woodpeckers in eastern deciduous forests ranges between 70% and 80% (Ingold 1989, Rodewald et al. 2005), but neither study occurred in burned forests. Dixon and Saab (2000) noted high nest success (87%) for Black-backed Woodpeckers (*Picoides arcticus*), which are primarily associated with burned areas. Saab and Vierling (2001) reported similarly high nest success rates for Lewis's Woodpeckers in a recently burned forest in Idaho. Predator communities differ between the Black Hills and other western coniferous forests (Gentry 2006), which likely explains geographical differences in predation rates and associated nesting success for Red-headed Woodpeckers.

Within the area affected by the Jasper fire, Red-headed Woodpecker nests occurred in snags, and larger snags (average = 27.4 cm dbh) were a critical component of Red-headed Woodpecker nest-site selection. The importance of snags has been reported elsewhere (Ingold 1989, Sedgwick and Knopf 1990), and the relative importance of larger snags is consistent with other studies. For instance, Gutzwiller and Anderson (1987) found that Red-headed Woodpeckers consistently chose larger snags than were generally available in the landscape. This preference for large snags may be contributing to population declines, given that snag sizes in the Black Hills are generally small (Spiering and Knight 2005) and aspens in general are rare. High-severity fire may be particularly important for aspen retention, since aspen regeneration is prolific in areas that have experienced high-severity fire (Shepperd 2001). While burned aspen stands were an important habitat for Red-headed Woodpeckers in this study, we do not know the relative importance of aspen to Red-headed Woodpeckers compared to other forest types in the Black Hills since we did not survey unburned sites. Spiering and Knight (2005) did not record any Red-headed Woodpeckers in their survey of managed, unburned forests in the Black Hills, which suggests that unburned pine-dominated forests in the Black Hills may not generally provide suitable breeding habitat for this species.

TABLE 2. Model selection based on logistic regression to predict Red-headed Woodpecker nest-site selection. The global model and models with $\Delta AIC_c \leq 4.0$ are presented below. K is the number of parameters in the model, ΔAIC_c is the difference between the AIC_c score for a given model and the lowest AIC_c, and Akaike weights are estimates of relative support for each model and sum to one. Please refer to Table 1 for covariate descriptions.

Candidate model	Log likelihood	K	ΔAIC_c[a]	Akaike weight (w_i)
dbh, distance to edge, % high-severity fire	−13.11	4	0	0.66
dbh, distance to edge, % high-severity fire, snag density	−12.75	5	3.4	0.12
dbh, distance to edge, % high-severity fire, shrub density	−12.86	5	3.6	0.11
Global model: dbh, shrub density, snag density, distance to edge, % high-severity fire	−12.53	6	7.9	0.01

[a] The lowest AIC_c score was 37.6.

The majority of Red-headed Woodpecker nests occurred in aspen groves that burned at high severity, and selection of nest sites within these aspen groves was likely due to the combined effects of snag creation and the formation of a productive understory. The recovery of aspen stands after exposure to high-severity fire was different than that of adjacent pine stands that burned at similar severity. Aspen groves are generally moister than the surrounding pine forest matrix, and while high-severity fire generally killed all affected pines, it rarely killed all aspen individuals in a grove. Following the Jasper fire, sprouting of aspen and other shrubs such as snowberry (*Symphoricarpos* sp.) was higher in severely burned aspen stands than in aspen stands that burned at low or moderate severity (Lentile 2004). Additionally, understory and shrub growth following the fire was higher in aspen stands that burned at high severity than in surrounding burned pine forest (Lentile 2004). This rapid recovery in severely burned aspen stands likely created an understory that supported a high density of arthropods relative to the surrounding pine forest.

Red-headed Woodpeckers nests were farther from edges than random sites. One potential explanation for this pattern relates to predation, which was the major factor influencing Red-headed Woodpecker nesting success following the Jasper fire. Other studies have noted that distance to an edge may affect nest predation rates, but that edge effects often differ with landscape setting, predator community, and patch characteristics (Wilcove 1985, Robinson et al. 1995, Hannon and Cotterill 1998). Alternatively, nests that are located in the "interior" of a stand likely differ in microclimate (Chen et al. 1993), which can affect arthropod densities. Given our limited sample size, we are unable to analyze the effects of a variety of covariates on nest survival following methods recently proposed by Shaffer (2004).

Our sample size was small (n = 17 nests), which reflects the fact that Red-headed Woodpeckers were not common in areas burned by the Jasper fire. Due to the nature of our surveys and the conspicuous nature and appearance of Red-headed Woodpeckers, it is unlikely that we missed nesting pairs. Rather, we believe that they were rare in this recently burned forest setting, and that additional studies are necessary to evaluate their relative use of different habitat types in the Black Hills.

This study suggests that interactions between burn severity and cover type are important, which is consistent with another recent study that noted that moderate–high severity fires may be important for other woodpecker species such as Northern Flickers (*Colaptes auratus*; Smucker et al. 2005). Given the decline of Red-headed Woodpeckers at a continental scale is undoubtedly due to a wide variety of factors, we suggest that additional studies are needed to address habitat selection and nest survival in a range of forested landscapes.

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