

NEST SUCCESS OF BLACK-BACKED WOODPECKERS IN FORESTS WITH MOUNTAIN PINE BEETLE OUTBREAKS IN THE BLACK HILLS, SOUTH DAKOTA

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Abstract. Black-backed Woodpeckers (*Picoides arcticus*) are burned-forest specialists that rely on beetles (Coleoptera) for food. In the Black Hills, South Dakota, standing dead forests resulting from mountain pine beetle (*Dendroctonus ponderosae*) outbreaks offer food resources for Black-backed Woodpeckers, in addition to providing habitat similar to burned forest. However, data on reproductive rates in these habitats are lacking. We estimated nest success and evaluated factors affecting nest survival of Black-backed Woodpeckers in beetle-killed forests in the Black Hills in 2004 and 2005. Nest success was 78% ($n = 12$) in 2004 and 44% ($n = 31$) in 2005. Fledging rates per pair were 2.0 ± 0.3 SE ($n = 12$) and 1.4 ± 0.3 SE ($n = 28$) in 2004 and 2005, respectively. Our results showed that temporal effects (e.g., age, date, and year) had the greatest influence on nest survival. Nest age was the most important predictor of daily nest survival; survival was higher in older nests. Nest survival was also lower later in the breeding season. The difference in nest success between the two years requires further study; however, nest success of Black-backed Woodpeckers in beetle-killed forests in the Black Hills was within the range of nest success within postfire habitats in this area. In the Black Hills, forests experiencing beetle outbreaks offer available habitat for Black-backed Woodpeckers.

Key words: Black Hills, Black-backed Woodpecker, logistic exposure, mountain pine beetle, nest success, nest survival, *Picoides arcticus*.

Éxito Reproductivo de *Picoides arcticus* en Bosques con Erupciones de Escarabajos *Dendroctonus ponderosae* en las Black Hills, South Dakota

Resumen. Los carpinteros de la especie *Picoides arcticus* son especialistas de bosques quemados que dependen de escarabajos (Coleoptera) como alimento. En las Black Hills, South Dakota, los bosques que quedan muertos en pie como resultado de las erupciones del escarabajo del pino montano (*Dendroctonus ponderosae*) ofrecen alimento para *P. arcticus*, además de proveer un hábitat similar al del bosque quemado. Sin embargo, no existen datos sobre las tasas reproductivas en esos hábitats. Estimamos el éxito de anidación y evaluamos los factores que afectan la supervivencia de los nidos de *P. arcticus* en bosques afectados por escarabajos en las Black Hills en 2004 y 2005. El éxito de los nidos fue del 78% ($n = 12$) en 2004 y del 44% ($n = 31$) en 2005. Las tasas de emplumamiento por pareja fueron de 2.0 ± 0.3 EE ($n = 12$) y 1.4 ± 0.3 EE ($n = 28$) en 2004 y 2005, respectivamente. Nuestros resultados mostraron que los efectos temporales (e.g., edad, fecha y año) tuvieron la mayor influencia sobre la supervivencia de los nidos. La edad del nido fue el factor que mejor predijo la supervivencia; ésta fue mayor en nidos más viejos. Además, la supervivencia fue menor conforme avanzó la época reproductiva. La diferencia en el éxito de anidación entre los dos años requiere más estudios. Sin embargo, el éxito reproductivo de *P. arcticus* en los bosques afectados por escarabajos en las Black Hills estuvo dentro del rango de éxito reproductivo documentado para ambientes quemados en esta área. En las Black Hills, los bosques que sufren las erupciones de los escarabajos ofrecen hábitat disponible para *P. arcticus*.

INTRODUCTION

Black-backed Woodpeckers (*Picoides arcticus*) are considered burned-forest specialists (Dixon and Saab 2000) that rely on beetles (Coleoptera) for food (Powell 2000, Bonnot 2006). In the Rocky Mountains, they are considered one of the most specialized bird species, found almost exclusively in forests recently burned by stand-replacing fires (Raphael and White

1984, Hutto 1995, Smucker et al. 2005). This specialization in postfire habitat amidst suppression of historical fire regimes throughout their range (Saab and Powell 2005) has resulted in the listing of Black-backed Woodpeckers as a species of management concern by state and federal agencies. In South Dakota, they are listed as locally rare and vulnerable to extinction and consequently as one of the Species of Greatest Concern in the Black Hills ecoregion (South Dakota Department of

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Game, Fish and Parks 2006). Currently, they are also listed by the U.S. Forest Service as a "Sensitive Species" for the Rocky Mountain region (USDA Forest Service 1996).

Similarly to fire, mountain pine beetle (*Dendroctonus ponderosae*) populations are a source of large-scale disturbance in the Black Hills (Shinneman and Baker 1997). Standing dead forests resulting from beetle outbreaks contain abundant snags that provide food in the form of the larvae of mountain pine beetles (Scolityidae) and wood borers (Buprestidae and Cerambycidae). Food and nesting resources in beetle-killed forests might explain why Black-backed Woodpeckers have been reported using these areas for breeding in other regions (Bull et al. 1986, Goggans et al. 1989, Setterington et al. 2000), and why, in the Black Hills, Black-backed Woodpeckers were the most common primary cavity-nesting species during a recent outbreak, with densities of nesting pairs as high as 3.6 per 40 ha (MAR, unpubl. data).

Forest managers in the Black Hills have an interest in beetle-killed forests given interest in logging. Recent changes to management activities in the Black Hills National Forest place more emphasis on reducing fire and insect hazards to timber (USDA Forest Service 2005). Such activities could affect conservation efforts for Black-backed Woodpeckers (Saab and Dudley 1998, Hutto and Gallo 2006, Saab et al. 2007). Given this potential conflict, there is a need to understand Black-backed Woodpecker reproduction and survival in these areas. However, little data on demographics exist for Black-backed Woodpeckers in areas of beetle outbreaks (but see Goggans et al. 1989). Our objective was to simultaneously estimate nest success and evaluate factors correlated with the nest success of Black-backed Woodpeckers in forests with outbreaks of mountain pine beetles in the Black Hills, South Dakota.

METHODS

STUDY AREA

We conducted our study in the Black Hills National Forest in the Black Hills region of southwestern South Dakota (43°10' to 44°50'N and 103°20' to 104°50'W; Froiland 1978). Elevation in the Black Hills ranges from 1066 m to 2207 m. The Black Hills are dominated by stands of ponderosa pine (*Pinus ponderosa*), but also include white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*; Hoffman and Alexander 1987).

Mountain pine beetle populations are prevalent in the Black Hills and consistently occur at endemic levels, with periodic outbreaks at epidemic levels about every 10 years and lasting 8–13 years (Blackman 1931, Allen 2005). Mountain pine beetles caused extensive ponderosa pine mortality throughout the Black Hills in the six years leading up to our study (Harris 2005). Surveys detected large and expanding areas of outbreaks in the Beaver Park and Bear Mountain areas starting in the late 1990s (Allen 2005). The outbreak in Beaver Park resulted in as many as 200–490 trees killed per hectare from 1998

to 2002 (Allen and Long 2001). By 2004, beetle populations were elevated across the entire Black Hills, with the northern and central portions experiencing tree mortality at epidemic levels resulting from coalescing areas of outbreak (Harris 2005). Aerial surveys indicated that over 27 000 ha of forests experienced outbreaks in 2004 (U.S. Forest Service, unpubl. data). Thirty-two percent of outbreaks occurred in patches greater than 100 ha in size. For comparison, during the three years from 2002 to 2004, the Black Hills experienced six fires that burned a total of 19 746 ha (USDA Forest Service 2008).

For the 2004 field season, we identified 58 potential study sites using aerial surveys from a fixed-wing aircraft flown over the central and northern regions of the Black Hills in March 2004. We located areas with beetles present by the discoloration of foliage on dead ponderosa pines resulting from tree mortality two years prior. However, aerial surveys provided only the location of outbreaks in 2004, without information about their size or extent. For the 2005 field season, we identified 54 study sites from remotely sensed imagery (USDA–Farm Service Agency, Aerial Photography Field Office, Salt Lake City, Utah) **taken in the fall of the previous year. This process was somewhat subjective, as forests containing mountain pine beetles are a heterogeneous distribution of variously aged snags and live trees, which complicates delineation of boundaries and differentiation among sites.** Nevertheless, sites identified for the 2005 field season averaged 195 ± 37 (SE) ha, but ranged from 3 ha to ≥ 1000 ha.

NEST MONITORING

We conducted area searches for nests in $\geq 90\%$ of the identified study sites from 22 April to 1 July in 2004 and 2005. We searched sites by spacing 2–4 crew members at distances of >100 m and walking transects through the area. We used call playbacks at intervals of 100–200 m to locate woodpeckers. Call playbacks consisted of a recorded sequence of three Black-backed Woodpecker vocalizations: a series of chirps, a series of three drums, and a series of three rattles. We paused recordings for 10–20 sec between separate vocalizations to listen for responses. Once found, we used behavioral cues to follow individuals until we located a nest. We recorded Universal Transverse Mercator coordinates for all nests using handheld global positioning system (GPS) units with an accuracy ≤ 10 m. We marked nests by flagging a tree at least 5 m from the nest tree and labeling the flag with the azimuth and height to the nest cavity.

We monitored nests every two days using video cavity viewers (Proudfoot 1996). On each visit we recorded the nest contents, date, time, and the stage of nesting (laying, incubation, or nestling) by observing parental behavior and nest contents. We continued monitoring the nest until success or failure. We considered a nest successful if ≥ 1 nestling fledged. We assumed a nest was successful if we observed broods in the area or if on the visit prior to finding an empty nest we

observed nestlings to be fully developed and close to fledging based on visual observation. Upon failure of a nest, we attempted to identify the cause by inspecting the cavity and its entrance and removing and inspecting any remaining nest contents. We considered a nest depredated if all eggs or nestlings disappeared or egg damage occurred (eggs or eggshell fragments found within the vicinity of the nest tree). We considered a nest abandoned if the pair no longer attended the nest but contents were intact.

To calculate the age of nests already containing eggs or young when found, we assumed females laid one egg a day (TWB, unpubl. data). We assumed a nine-day incubation period (beginning on the day the last egg was laid) and a 24-day nestling period (beginning on the day the first egg hatched), which we obtained by averaging across nests in our sample with known incubation and nestling period lengths (length of incubation = 9.3 ± 0.2 [SE] days [$n = 16$]; length of nestling period = 23.9 ± 0.42 [SE] days [$n = 19$]). We used characteristics of plumage development of nestlings of known age recorded on each visit to estimate the ages of nests that were found in the nestling stage and failed before completion.

VEGETATION MEASUREMENTS

Following the completion of each nesting attempt, we measured vegetation characteristics at the nest site. Using a measuring tape and a telescoping pole, we measured nest height from the ground to the center of the cavity entrance (to the nearest 0.01 m). We recorded tree species and diameter at breast height (dbh, to the nearest 0.01 m) of each nest tree. Each nest tree was assessed as either live or dead. We calculated the average percentage of overstory canopy closure using a moosehorn (Garrison 1949) at 49 points around each nest, including one point at the nest site and 12 on each of the four cardinal axes at 1 m intervals. We tabulated numbers of all stems ≥ 2.5 cm dbh and ≥ 1.4 m tall inside a fixed-radius (12.5 m) plot (Mannel et al.

2006) centered on each nest tree. We calculated the distance (to the nearest 5 m) from each nest tree to the nearest edge (defined as a boundary between closed canopy forest, live or dead, and an opening of any kind, e.g., a clear-cut or a meadow) using digital orthoquad images in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, California).

We calculated indices of food availability in the nest plot and an additional 80 plots arranged at 50 m intervals on 16 transects, radiating out from the nest at increments of 22.5° . In each plot we recorded the density of trees containing mountain pine beetles. Similarly to Powell et al. (2002), we obtained an index of wood borer abundance by counting egg niches (Furniss 1980) within a 30.5 cm wide strip at a height of 1.7 m around the circumference of all pine snags ≤ 2 years old within the plot.

STATISTICAL ANALYSES

We used an information-theoretic framework (Burnham and Anderson 2002) to evaluate support for 13 models identified as possibly influencing Black-backed Woodpecker nest survival. Our models primarily considered combinations of temporal effects, including year, ordinal date, and nest age (from the day the first egg was laid until completion; Table 1). However, given the importance of prey in various aspects of Black-backed Woodpecker ecology, for example, foraging- and nest-site selection (Caton 1996, Powell 2000), nest success might be related to available food resources. Therefore, we also evaluated models containing the density of trees containing mountain pine beetles and indices of wood borer abundance as covariates. Lastly, we fit models with covariates describing habitat characteristics that could influence nest concealment and predation rates. These variables included mean overstory canopy closure in the nest plot, distance from the nest tree to the nearest edge, cavity height, nest tree species, and stem densities in the nest plot (Table 1).

TABLE 1. Descriptions of variables used in candidate models examining variation in Black-backed Woodpecker nest survival in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004 and 2005.

Hypothesis	Variable	Description
Temporal	AGE	Age (days) of nest from laying of first egg
	DATE	Ordinal date
	YEAR	2004 or 2005
Habitat	CAVHT	Height above ground of center of cavity entrance hole (m)
	SPECIES	Species of nest tree (pine or aspen)
	OCC	Mean percent of overstory canopy closure from 49 observations on cardinal axis of nest plot
	STEM	Density (per ha) of all stems > 2.5 cm diameter at breast height (dbh) and > 1.4 m tall occurring in 12.5 m radius plot centered on nest
	DIST	Distance from nest tree to nearest edge (m); edge defined as boundary between closed canopy forest and opening of any kind
Food	MPB	Average density (per ha) of trees (≥ 10 cm dbh) with mountain pine beetles in 80 12.5 m radius plots surrounding the nest
	WB	Index of wood borer abundance within 250 m of nest tree (from egg niche counts in 31 cm wide strip of bark at height of 1.7 m on all pine snags dead ≤ 2 years)

We used the logistic-exposure method to estimate nest survival (Shaffer 2004). In this model, the daily survival rate (DSR) is modeled using an appropriate predictor function, in this case, the S-shaped logistic function, with the form:

$$s(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}$$

Although similar to the logistic regression model, the link function differs by containing an exponent ($1/t_{ij}$) in both the denominator and numerator. This exponent directly considers that the probability of surviving an interval relates to interval length (Shaffer 2004). We used PROC GENMOD (SAS Institute 2004) to fit logistic-exposure models to our data. We screened explanatory variables for multicollinearity using tolerance values (PROC REG; Allison 1999, SAS Institute 2004). We evaluated the goodness-of-fit of the global model using the Hosmer and Lemeshow (2000) goodness-of-fit test.

We compared and ranked nest survival models using Akaike's information criterion corrected for small sample size (AIC_c), calculated from the effective sample size (Burnham and Anderson 2002, Rotella et al. 2004). We computed Akaike weights (w_i) for each model, where w_i represents the probability of a model being the best approximating model of those evaluated (Burnham and Anderson 2002). We addressed model selection uncertainty by calculating model-averaged estimates of the coefficients as:

$$\hat{\beta} = \sum_{i=1}^R w_i \hat{\beta}_i$$

where $\hat{\beta}$ is the model averaged estimate of the coefficient, w_i is the Akaike weight computed from AIC_c values for only the R competing models containing the specific predictor variable, and $\hat{\beta}_i$ is the estimator of the coefficient for a specific variable in model i (Burnham and Anderson 2002). We calculated unconditional standard errors for model-averaged coefficients (Burnham and Anderson 2002) using:

$$SE(\hat{\beta}) = \sqrt{\widehat{\text{var}}(\hat{\beta})}$$

where

$$\widehat{\text{var}}(\hat{\beta}) = \left[\sum_{i=1}^R w_i \sqrt{\widehat{\text{var}}(\hat{\beta}_i) + (\hat{\beta}_i - \hat{\beta})^2} \right]^2$$

We averaged across all models with a weight $\geq 1/8$ th of the weight of the top model (Burnham and Anderson 2002). We estimated the relative importance of covariates from averaged models by summing the Akaike weights across all competing models in which the covariate occurred (Burnham and Anderson 2002).

To evaluate the predictive ability of our daily nest survival model, we used a modification to the k-fold cross-validation design of Boyce et al. (2002). We divided the nest data set into five random subsets (20% of the total data). We successively removed one subset (the testing set) and recalculated the model

using the remaining data (training set). Validation was based on the remaining testing set containing only successful nest monitoring intervals. We assessed the model's performance by comparing the distribution of predicted DSRs for the testing data against categories (bins) of DSRs using a Spearman-rank correlation between the frequencies of nest monitoring intervals within individual bins and the bin rank (Boyce et al. 2002). We designated DSR bins by creating 10 equal intervals between the maximum and minimum DSR calculated from the training data. We would expect a model with good predictive ability to have a strong, positive correlation, as higher frequencies occur in higher DSR bins (Boyce et al. 2002).

We interpreted the effects of explanatory variables on survival using the odds ratios and 95% confidence intervals of model-averaged estimates (Hosmer and Lemeshow 2000). We estimated model-averaged DSRs and nest success rates by varying explanatory variables of interest while holding other variables at fixed values. We calculated nest success as the product of DSRs for each day in the nesting period (Shaffer and Thompson 2007). We assumed the length of the nesting period to be 37 days (assuming a four-day laying period, nine days of incubation, and a 24-day nestling stage; TWB, unpubl. data). If survival varied with date, we estimated overall nest success by taking a weighted average of the proportion of nests initiated on a given date and the individual nest success associated with that date of initiation across all dates on which nests were initiated (Shaffer and Thompson 2007). We report fledging rates and nest success estimates as mean \pm SE.

RESULTS

Our analysis included 43 nests over two years: 12 nests in nine sites in 2004, and 32 nests in 12 sites in 2005; however, we only sampled vegetation around 31 nests in 2005. Nest density in sampled sites in 2005 was 0.13 nests per 40 ha. Two (17%) and 17 (53%) nests failed in 2004 and 2005, respectively. Predation was the leading cause of nest loss (89%), with 10 predation events occurring during incubation, and seven during the nestling stage. The identity of predators was unknown, but evidence included nestling remains and damage to cavity entrances. Two nests were abandoned, both during the incubation period.

Number of fledglings per pair in 2004 was 2.0 ± 0.3 ($n = 12$). In 2005, Black-backed Woodpecker nests fledged 1.2 ± 0.2 young per nesting attempt ($n = 32$). However, in 2005 we confirmed renesting by four pairs following failure of their first nest. Adjusted fledging rates accounting for observed renesting increased productivity in 2005 to 1.4 ± 0.3 ($n = 28$).

The global model adequately fit the data ($\chi^2_8 = 7.2$, $P = 0.99$). No single model received overwhelming support, however temporal models were most supported (Table 2). The daily nest survival model derived from the six variables in the top models (Table 3) had strong predictive ability ($r_s = 0.84$, $P < 0.001$).

TABLE 2. Support for logistic exposure models predicting Black-backed Woodpecker nest survival in the Black Hills, South Dakota, 2004–2005. K is the number of parameters in the model, $-2\log(\mathcal{L})$ is -2 times the log-likelihood estimator, AIC_c is Akaike’s information criterion adjusted for small sample size, Δ_i is the difference in AIC_c value from that of the top model, and w_i is the Akaike weight. See Table 1 for explanations of model variables.

Model	$-2\log(\mathcal{L})$	K	Δ_i	w_i
AGE + DATE ^{a,b}	-78.06	3	0.00	0.29
AGE + YEAR ^b	-78.57	3	1.01	0.18
AGE + DATE + YEAR ^b	-77.64	4	1.17	0.16
DATE + YEAR ^b	-79.02	3	1.92	0.11
CONSTANT ^b	-81.51	1	2.87	0.07
DATE ^b	-80.77	2	3.40	0.05
WB ^b	-81.13	2	4.12	0.04
CAVHT + SPECIES	-80.20	3	4.27	0.03
DIST + SPECIES	-80.26	3	4.40	0.03
MPB	-81.51	2	4.88	0.03
OCC + CAVHT + STEM	-80.98	4	7.84	0.01
DIST + STEM + OCC	-81.32	4	8.54	0.00
CAVHT + OCC + DIST + SPECIES + STEM	-79.90	6	9.73	0.00

^a AIC_c of the top model = 162.15.

^bModels with a w_i within 1/8th of the w_i of the top model were considered competing models and used in model averaging (Burnham and Anderson 2002).

Although temporal factors best predicted nest survival, their effects were variable (Table 3). Nest age and date were the most important predictors of nest survival (Table 3). The odds of daily nest survival decreased 2% per day over the course of the nesting period (odds ratio = 0.98), but increased 3% for each one-day increase in nest age (odds ratio = 1.03; Fig. 1). Year had the strongest effect on DSR, with nests in 2005 having a 42% lower chance of surviving a given day (odds ratio = 0.58).

Daily survival rates for 2004 ranged from 0.949 to 0.999, depending on date and nest age (Fig. 1). Daily survival rates in 2005 showed similar trends, but were lower, ranging from 0.893 to 0.998 (Fig. 1). Black-backed Woodpeckers experienced an overall nest success in 2004 of 78% ± 1% ($n = 12$), however in 2005 the success rate was much lower at 44% ± 0% ($n = 31$).

Estimated nest success was high (above 80%) for nests started early in the season (late April and early May), and decreased as a function of later nest initiation date.

DISCUSSION

Much of the ecology of Black-backed Woodpeckers appears to be driven by the availability of their main foods, bark and wood-boring beetles (Spring 1965, Yunick 1985, Dixon and Saab 2000). However, the model containing mountain pine beetle indices was not supported and the model related to wood borer availability received only weak support. Thus, although food is most likely an important consideration in the nesting ecology of Black-backed Woodpeckers (Hutto and Gallo 2006), our research suggests that its importance rests in nest-site selection (Bonnot 2006), rather than nest success. We hypothesize that food availability influences nest location (Bonnot 2006), but not whether a nest is successful, if birds select nest sites where food availability is high, such as a forest area experiencing a beetle outbreak. Given the lack of difference in beetle densities among nest sites, temporal factors ultimately influenced nest success in our study.

Nest age was the most important predictor of nest survival. Although we might have expected that predation would be the leading cause of nest mortality (Martin 1993), the positive association of age with DSR differs from other studies that have shown higher predation rates on older nests (Martin et al. 2000, Lloyd and Martin 2005). Prolonged exposure to predators and increased activity by parents and nestlings, whose begging calls can be heard from nests, are thought to be responsible for higher predation rates later in the nesting stage (Briskie et al. 1999, Martin et al. 2000). While the factors influencing the lower predation rates at later brood ages that we observed are unknown, possible explanations include increased parental defense as nestlings approach fledging (Montgomerie and Weatherhead 1988) or an increased ability of nestlings to defend themselves against predators (Bradley and Marzluff 2003).

Daily nest survival rates for Black-backed Woodpeckers decreased over the course of the nesting season. Fisher and Wiebe (2006) observed fluctuations in DSRs for Northern

TABLE 3. Model-averaged parameter estimates and unconditional standard errors (SE), odds ratios, odds ratio 95% confidence intervals (CI), and importance values explaining Black-backed Woodpecker nest survival in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004–2005. See Table 1 for explanations of parameters.

Parameter	Category level	Estimate	SE	Odds ratio	Lower CI	Upper CI	Importance
Intercept		7.53	3.07				
AGE		0.03	0.02	1.03	0.99	1.08	0.70
DATE		-0.02	0.02	0.98	0.95	1.01	0.63
YEAR	2004 ^a	0.00	0.00				0.61
	2005	-0.55	0.50	0.58	0.21	1.54	0.50
WB		-0.00	0.00	1.00	1.00	1.00	0.04

^aThis was the reference category in the analysis, consequently the estimate was set to 0.

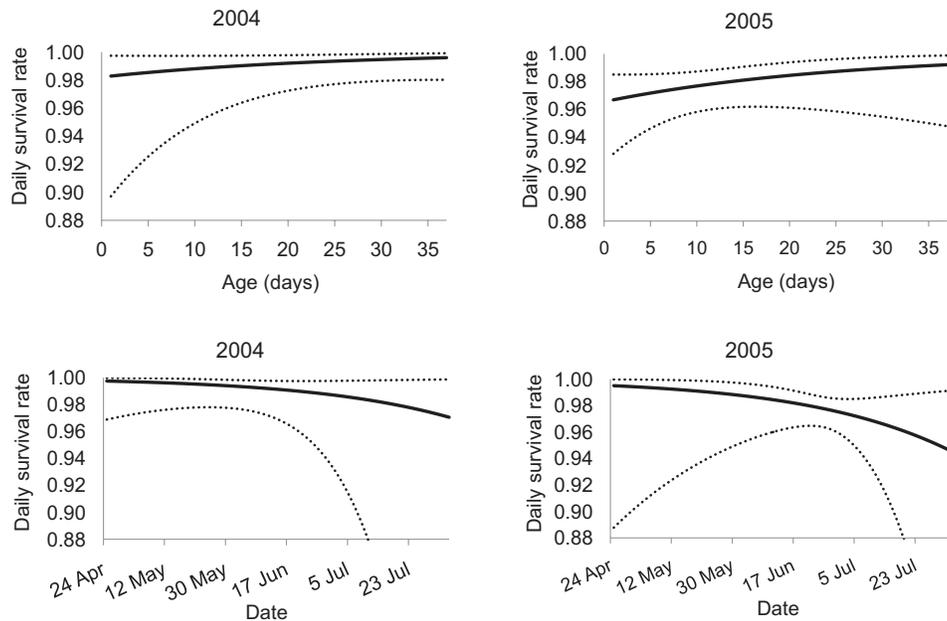


FIGURE 1. Nests of Black-backed Woodpeckers further along in the nesting cycle had higher estimated daily survival rates than younger nests, whereas nests initiated later in the breeding season had lower daily survival rates than those initiated earlier in the breeding season. Results are based on Black-backed Woodpecker nests in areas of mountain pine beetle outbreaks in the Black Hills, South Dakota, 2004 and 2005. Upper and lower 95% confidence limits are shown by dashed lines. Brood age was held at 18 days when estimating survival rates across dates. Estimates for survival rates by age were made using 14 June as the date. The index of wood borer abundance was held at its mean.

Flickers (*Colaptes auratus*) throughout the breeding season, and speculated that variation in DSR with date may have been a function of predators switching food sources midseason. Others have linked lower nest success rates and reproductive performance to later egg-laying dates in cavity-nesters (Perrins 1996, Hogstad and Sternberg 1997, Fisher and Wiebe 2006). We were able to confirm half of the six nests that were active after 15 July as second nests. This suggests that a large proportion of the nesting activity occurring late in the breeding season may be renesting attempts. Of the renesting attempts that we observed ($n = 4$), only 50% successfully fledged young. A higher potential for failure of renesting attempts may be due to reduced parental care, resulting from the increased energetic demands on parents that attempt to renest (Fisher and Wiebe 2006). Alternatively, it may be that the ability or behavior of individuals or pairs whose first nest attempts failed predispose them to lower nest success (Witkander et al. 2001).

Cavity-nesting birds typically have nest success rates greater than 50%, but rates can vary from as low as 25% to 100% (Martin and Li 1992). Previous studies have indicated that nest success for Black-backed Woodpeckers may be lower in beetle-killed forests than in recently burned forests. Success rates reported for burned forests were 87% in Idaho, 100% in Wyoming, and 71% Montana (Dixon and Saab 2000). Although our estimates differed considerably from 2004 to

2005, nest success for Black-backed Woodpeckers in beetle-killed forests in the Black Hills was lower than that reported for burned sites. However, our nest success results were similar, although lower in 2005, to those of Vierling et al. (2008), who recently reported success rates of 50%, 60%, and 80% for Black-backed Woodpeckers in low, moderate, and high severity burn patches, respectively, in a large burned forest in the region. In addition, the fledging rates we observed were similar to the 1.6 ± 0.2 SE per pair per year ($n = 14$) reported by Dixon and Saab (2000) for burned forests.

The extent of Black-backed Woodpecker nesting in mountain pine beetle outbreaks in the Black Hills has previously gone undocumented. Our estimate of nest density in these sites in 2005 is slightly greater than what was recently reported for burned forest in the region (0.1 nests per 40 ha; Vierling et al. 2008). Furthermore, our sample of Black-backed Woodpecker nests, which is the largest two-year sample size that we are aware of, fledged young at rates comparable to those in burned forests. While the disparity in nest success between years leaves much to be confirmed, as does the lack of information on adult and juvenile survivorship, which is needed to fully assess the utility of these sites to Black-backed Woodpeckers, our results suggest that forests affected by beetle outbreaks provide nesting habitat for Black-backed Woodpeckers in the Black Hills. As a result, managers may be challenged to consider the

trade-offs between Black-backed Woodpecker habitat conservation and forest management that targets mountain pine beetle outbreaks. Given the infrequency of large-scale, stand-replacing fires in our study area, further work is needed to understand the importance of beetle-killed forests in the maintenance of Black-backed Woodpecker populations in this region.

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LITERATURE CITED

- ALLEN, K. K. 2005. Evaluation of mountain pine beetle activity in the Deerfield area of the Black Hills National Forest. USDA Forest Service, Biological Evaluation R2-04-01.
- ALLEN, K. K., AND D. F. LONG. 2001. Evaluation of mountain pine beetle activity on the Black Hills National Forest. USDA Forest Service, Biological Evaluation R2-02-02.
- ALLISON, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Inc., Cary, NC.
- BLACKMAN, M. W. 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopkins). Technical Publication No. 36, New York State College of Forestry, Syracuse, NY.
- BONNOT, T. W. 2006. Nesting ecology of Black-backed Woodpeckers in mountain pine beetle infestations in the Black Hills, South Dakota. M.Sc. thesis, University of Missouri, Columbia, MO.
- BOYCE, M. S., P. R. VERNIER, S. E. NIELSEN, AND F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. *Ecological Modeling* 157:281–300.
- BRADLEY, J. E., AND J. M. MARZLUFF. 2003. Rodents as nest predators: influences on predatory behavior and consequences for nesting birds. *Auk* 120:1180–1187.
- BRISKIE, J. V., P. R. MARTIN, AND T. E. MARTIN. 1999. Nest predation and the evolution of nestling begging calls. *Proceedings of the Royal Society of London Series B* 266:2153–2159.
- BULL, E. L., S. R. PETERSON, AND J. W. THOMAS. 1986. Resource partitioning among woodpeckers in northeastern Oregon. USDA Forest Service, Pacific Northwest Research Station, Research Note PNW-RN-444.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CATON, E. L. 1996. Effects of fire and salvage logging on the cavity-nesting bird community in northwestern Montana. Ph.D. dissertation, University of Montana, Missoula, MT.
- 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.
- FISHER, R. J., AND K. L. WIEBE. 2006. Nest site attributes and temporal patterns of Northern Flicker nest loss: effects of predation and competition. *Oecologia* 147:744–753.
- FROILAND, D. G. 1978. Natural history of the Black Hills. The Center for Western Studies, Augustana College, Sioux Falls, SD.
- FURNISS, R. L. 1980. Western forest insects. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Miscellaneous Publication 273.
- GARRISON, G. A. 1949. Uses and modifications for the “Moosehorn” crown closure estimator. *Journal of Forestry* 47:733–735.
- GOGGANS, R., R. D. DIXON, AND L. C. SEMINARA. 1989. Habitat use by Three-toed and Black-backed Woodpeckers, Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife, Technical Report 87-3-02, Portland, OR.
- HARRIS, J. L. 2005. Forest insect and disease conditions in the Rocky Mountain Region, 2004. USDA Forest Service, Rocky Mountain Region, Renewable Resources R2-05-09.
- HOFFMAN, G. R., AND R. R. ALEXANDER. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-RP-276.
- HOGSTAD, O., AND I. STERNBERG. 1997. Breeding success, nestling diet and parental care in the White-backed Woodpecker (*Dendrocopos leucotos*). *Journal of Ornithology* 138:25–38.
- HOSMER, D. W., JR., AND S. LEMESHOW. 2000. Applied logistic regression. John Wiley and Sons, New York.
- HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in the northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9:1041–1058.
- HUTTO, R. L., AND S. M. GALLO. 2006. The effects of postfire salvage logging on cavity-nesting birds. *Condor* 108:817–831.
- LLOYD, J. D., AND T. E. MARTIN. 2005. Reproductive success of Chestnut-collared Longspurs in native and exotic grassland. *Condor* 107:363–374.
- MANNEL, S., M. A. RUMBLE, M. PRICE, T. M. JUNTTI, AND D. HUA. 2006. Comparison of combinations of sighting devices and target objects for establishing circular plots in the field. USDA Forest Service Research Paper RM-RP-60.
- MARTIN, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. *Bioscience* 43:523–532.
- MARTIN, T. E., AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579–592.
- MARTIN, T. E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London Series B* 267:2287–2293.
- MONTGOMERIE, R. D., AND P. J. WEATHERHEAD. 1988. Risks and rewards of nest defense by parent birds. *Quarterly Review of Biology* 63:167–187.
- PERRINS, C. M. 1996. Eggs, egg formation and the timing of breeding. *Ibis* 138:2–15.
- POWELL, H. D. W. 2000. The influence of prey density on postfire habitat use of the Black-backed Woodpecker. M.Sc. thesis, University of Montana, Missoula, MT.
- POWELL, H. D. W., S. J. HEJL, AND D. L. SIX. 2002. Measuring woodpecker food: a simple method for comparing wood-boring beetle abundance among fire-killed trees. *Journal of Field Ornithology* 73:130–140.
- PROUDFOOT, G. A. 1996. Miniature video-board camera used to inspect natural and artificial nest cavities. *Wildlife Society Bulletin* 24:528–530.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity nesting birds in the Sierra Nevada. *Wildlife Monographs* 86.
- ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:187–208.

- 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 H. POWELL [EDS.]. 2005. Fire and avian ecology in North America. *Studies in Avian Biology* 30.
- SAAB, V. A., R. E. RUSSELL, AND J. G. DUDLEY. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. *Condor* 109:97–108.
- SAS INSTITUTE. 2004. SAS/STAT user's guide. Version 9. SAS Institute, Inc., Cary, NC.
- SETTINGINGTON, M. A., I. D. THOMPSON, AND W. A. MONTEVECCHI. 2000. Woodpecker abundance and habitat use in mature balsam fir forests in Newfoundland. *Journal of Wildlife Management* 64:335–345.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- SHAFFER, T. L., AND F. R. THOMPSON III. 2007. Making meaningful estimates of nest survival with model-based methods. *Studies in Avian Biology* 34:84–95.
- SHINNEMAN, D. J., AND W. L. BAKER. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conservation Biology* 11:1276–1288.
- SMUCKER, K. M., R. L. HUTTO, AND B. M. STEELE. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15:1535–1549.
- SOUTH DAKOTA DEPARTMENT OF GAME, FISH AND PARKS. 2006. South Dakota comprehensive wildlife conservation plan. Wildlife Division Report 2006–08, South Dakota Department of Game, Fish and Parks, Pierre, SD.
- SPRING, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. *Condor* 67:457–488.
- USDA FOREST SERVICE. 1996. Final environmental impact statement. Black Hills National Forest Land Resource Management Plan, USDA Forest Service, Custer, SD.
- USDA FOREST SERVICE. 2005. Record of Decision, Final Environmental Impact Statement, Phase II Amendment, 1997 Revised Land Resource Management Plan, Black Hills National Forest. USDA Forest Service, Custer, SD.
- USDA FOREST SERVICE [ONLINE]. 2008. Black Hills National Forest historical fire information. <<http://www.fs.fed.us/r2/blackhills/fire/>> (4 April 2008).
- VIERLING, K. T., L. B. LENTILE, AND N. NIELSEN-PINCUS. 2008. Pre-burn characteristics and woodpecker use of burned coniferous forests. *Journal of Wildlife Management* 72:422–427.
- WIKTANDER, U., O. OLSSON, AND S. G. NILSSON. 2001. Age and reproduction in Lesser Spotted Woodpeckers (*Dendrocopos minor*). *Auk* 118:624–635.
- YUNICK, R. P. 1985. A review of recent irruptions of the Black-backed Woodpecker *Picoides arcticus* and Three-toed Woodpecker *Picoides tridactylus* in eastern North America. *Journal of Field Ornithology* 56:138–152.