



NEST-SITE SELECTION IN A POSTFIRE LANDSCAPE: DO PARENTS MAKE TRADEOFFS BETWEEN MICROCLIMATE AND PREDATION RISK?

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ABSTRACT.—Maternal preference for nest sites is predicted to be an adaptive consequence of selective pressures acting on parents and young at the nest site. Nest predation risk has been linked to nest-site placement in birds, but microclimatic extremes can impose fitness costs on both adults and young, and these two factors may conflict. I used the temporal and spatial variation in microclimatic conditions and nest predation risk generated by variation in wildfire severity to examine the relationship between nest-site preference, nest microclimate, and fitness costs to parents and young in the Dark-eyed Junco (*Junco hyemalis*), a facultative cavity-nester. Adults preferred to select exposed nest sites oriented toward the north—sites that consistently had the most moderate thermal regimes. Nestlings reared in burrow-type nests gained mass more slowly and experienced retarded skeletal growth compared with exposed nests, but slower growth was not explained by suboptimal nest temperatures, nestling provisioning rates, or nest attentiveness. Although young raised in the warmest nest sites (exposed and south-facing) did not experience reduced growth rates as predicted, incubating females reduced their nest attentiveness and parents increased their nestling provisioning rate at these nest sites. The results suggest that nest microclimate can affect thermoregulatory costs to parents and offspring that can influence parental care decisions. Variation in nest predation was unrelated to microclimatic characteristics of nest sites, which suggests that parents do not make tradeoffs between microclimate and risk of nest predation when locating nests. *Received 3 August 2008, accepted 10 January 2009.*

Key words: cavity nesting, Dark-eyed Junco, *Junco hyemalis*, nest attentiveness, nest microclimate, temperature, wildfire.

Selección de Sitios de Anidación en un Paisaje que ha sido Quemado: ¿Existe un Compromiso para los Padres entre el Microclima y el Riesgo de Depredación?

RESUMEN.—Se predice que las preferencias maternas por los sitios de anidación son una consecuencia adaptativa de las presiones de selección que actúan sobre los padres y las crías en dichos sitios. El riesgo de depredación de los nidos ha sido ligado a la ubicación de los sitios de anidación en las aves, pero los extremos microclimáticos pueden imponer costos sobre la adecuación de los adultos y de las crías, y esos dos factores pueden estar en conflicto. Usé la variación temporal y espacial en las condiciones microclimáticas y el riesgo de depredación de los nidos, generados por la variación en la severidad de los fuegos naturales, para examinar la relación entre la preferencia por sitios de anidación, el microclima de los nidos y los costos sobre la adecuación de los padres y las crías en *Junco hyemalis*, una especie que anida facultativamente en cavidades. Los adultos prefirieron seleccionar sitios de anidación expuestos y orientados hacia el norte, los cuales presentaron los regímenes térmicos más moderados de forma consistente. Los pichones que fueron criados en nidos tipo madriguera aumentaron de peso más lentamente y presentaron un crecimiento del esqueleto retardado en comparación con los pichones de nidos abiertos, pero su crecimiento más lento no pudo ser explicado por temperaturas subóptimas en los nidos, por las tasas de aprovisionamiento de los pichones ni por la atención brindada por los padres a los nidos. Aunque los pichones criados en los sitios de anidación más cálidos (expuestos y orientados hacia el sur) no presentaron tasas de crecimiento reducidas como se había predicho, las hembras incubantes disminuyeron su presencia en los nidos y los padres aumentaron su tasa de aprovisionamiento de los pichones en esos sitios de anidación. Los resultados sugieren que el microclima de los nidos puede afectar los costos de termorregulación para los padres y los pichones, y estos costos pueden influenciar las decisiones relacionadas con el cuidado parental. La variación en la depredación de los nidos no estuvo relacionada con características microclimáticas de los sitios de anidación, lo que sugiere que los padres no se enfrentan a un compromiso entre el microclima y el riesgo de depredación de los nidos al seleccionar lugares para anidar.

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THE ADAPTIVE SIGNIFICANCE of breeding-site preference in birds has been studied extensively, but research has largely focused on the predator-avoidance value of nest sites (Martin 1998). Indeed, depredation is the primary cause of nest failure in birds, particularly in passerines (Ricklefs 1969, Martin 1995). Improved concealment of nests commonly leads to reduced likelihood of depredation (e.g., Wray and Whitmore 1979, Møller 1988), so depredation is a source of selection on nest placement. Yet many abiotic factors in the environment also have the potential to shape nest-site preference (Goldsbrough et al. 2004).

Nest temperature, in particular, can have a major influence on energy and water budgets of both parents and developing young (Ricklefs and Hainsworth 1969, Dawson et al. 2005) and has been associated with nest-site preference in many studies (e.g., Viñuela and Sunyer 1992). Birds orient nests to allow direct insolation of overly cool nest sites (e.g., cavities; Austin 1974, Wiebe 2001), to avoid overheating of nests by direct sunlight (Burton 2006, Tieleman et al. 2008), and to increase nest cooling by prevailing winds during the heat of the day (Austin 1974, Hartman and Oring 2003). Cooler microsites are advantageous to incubating and brooding parents in that they reduce the need to cool or shade thermally stressed young (Lloyd and Martin 2004, Tieleman et al. 2008). Females that avoid overly hot nest sites are associated with larger clutch size (Wiebe 2001), enhanced hatching success (Viñuela and Sunyer 1992, Burton 2006), higher nestling growth rates (Lloyd and Martin 2004), and higher nestling survival (Austin 1974). Overly cold microsites (e.g., cavity nests), however, increase thermoregulatory costs on nestlings, which slows growth (Dawson et al. 2005). Collectively, these facts suggest that thermal extremes impose different costs on offspring and parents.

Relatively few studies have attempted to relate microclimatic variation associated with nest preference to both parental behavior and reproductive performance, and even fewer have examined multiple selective pressures or constraints on nest placement and how they translate into nest-site preference. Documenting links between nest predation, microclimate, and reproductive performance through effects on parents and offspring has great potential to increase our appreciation of microclimate as a selective force on nest-site selection.

Here, I approach this topic first by measuring nest-site preferences and the microclimatic characteristics of nest sites selected by Dark-eyed Juncos (*Junco hyemalis*; hereafter “juncos”) nesting in postfire forest habitat in the Northern Rocky Mountains. Wildfire has dramatic effects on forest structure when fire severity and extent vary over space (Turner et al. 2003) and creates gradients in canopy and groundcover that are known to affect the thermal regime of nest sites (With and Webb 1993, Lloyd and Martin 2004). The junco, a primarily ground- and open-cup-nesting songbird that is abundant across a range of fire severities in this region (Smucker et al. 2005), has likely evolved strategies for dealing with the dramatic temporal and spatial heterogeneity found in postfire environments. In fact, juncos are more abundant in recently burned forests than in any other land-cover type in the Northern Rockies (Hutto 1995), which suggests that postfire landscapes represent important settlement opportunities. Juncos are facultative cavity-nesters (Nolan et al. 2002) that select nest sites on open ground under vegetation (Martin 1998) and in other locations that are effectively underground. Thus, in postfire environments, juncos may

be faced with dramatic thermal gradients, but also with a wide range of nest-site options that are likely to differ in their thermal properties. I focus on nest orientation and type (burrow vs. exposed) as components of nest-site choice because the direction of the nest opening and its overall concealment determine the duration, timing, and extent of exposure to direct sun.

Next, I relate variation in nest microclimate associated with nest-site choice to components of reproductive performance (hatching success, nestling survival, and nestling growth rates) and two components of parental investment (nest attentiveness during incubation and nestling provisioning). Nestling growth rate is an important component of offspring fitness (Gebhardt-Henrich and Richner 1998) that is sensitive to temperature variation at nest sites (Dawson and O'Connor 1996, Lloyd and Martin 2004), but in altricial species it is ultimately limited by the ability of parents to provide food to fuel growth. Parents can experience increased thermoregulatory costs at thermally stressful nest sites (Haftorn and Reinertsen 1985, Tieleman et al. 2008) that reduce their ability to care for young (Conway and Martin 2000). Parents also may need to offset increased thermoregulatory costs to young by shading eggs or young and by providing additional food and water to nestlings. High nest attentiveness (percentage of time that a parent sits on the nest) is favored during incubation to prevent the increased mortality and reduced developmental rate of embryos associated with absence from the nest (White and Kinney 1974). However, if high nest temperatures overwhelm parents' thermoregulatory capabilities, placing nests in thermally stressful sites may constrain nest attendance, which can reduce nesting success or offspring fitness (Martin et al. 2007). Consequently, thermally stressful nest sites are likely to impose energetic demands on both parents and young that can shape the evolution of nest-site preferences through parental decisions regarding the allocation of energy to self-maintenance and parental care. Finally, I examine the relationship between structural characteristics of nest sites that shape microclimate and the likelihood of nest predation.

METHODS

Study site and study species.—The study was conducted in 2004–2005 within the boundaries of the 7,062-acre Black Mountain fire of 2003 in the Lolo National Forest near Missoula, Montana. The study area is a low- to moderate-elevation site dominated by mixed-conifer forest stands of Ponderosa Pine (*Pinus ponderosa*), Lodgepole Pine (*P. contorta*), and Western Larch (*Larix occidentalis*). I established a 300-ha subplot as the focal study area on the basis of its narrow elevational range (1,280–1,340 m), the presence of forest patches that burned at different severities, and its fine-scale interspersed of severities. Female juncos select nest sites and perform nearly all of the construction of open-cup nests (Nolan et al. 2002). Only females incubate (Wolf et al. 1991), but both sexes feed nestlings (Ketterson et al. 1992).

Nest-site selection and nest temperature.—I monitored each junco territory for the entire breeding season and searched daily for all junco nesting attempts from late April to early August each year. To examine patterns of nest-site selection, I measured the following variables immediately after the termination of a nesting attempt: nest concealment, nest orientation, percent canopy and groundcover, and burn severity. “Nest concealment” was defined

as a visual estimate of the percentage of the bowl of each nest that was visible from a distance of 1 m from each of the four cardinal directions and from directly above. All five directional measurements were averaged, yielding a single index of concealment for each nest. In postfire landscapes, juncos frequently nest in carbonized holes in the ground created by the incineration of tree roots (B. Robertson pers. obs.). Nests were categorized as "burrow nests" if >50% of the nest bowl was visually occluded from directly above by a roof of rock or soil.

"Nest orientation" was defined as the compass direction from which the greatest percentage of the nest bowl was visible (from a distance of 1 m at a 45° vertical angle), in relation to magnetic north, as the azimuth bisecting the direction of greatest exposure. Orientation was divided into four categories delineated by the ordinal directions (e.g., 1–90° = northeast). These categories reflect four distinct temperature regimes shaped by the azimuth angle of the sun (Lloyd and Martin 2004): northeastern orientations receive direct sun only immediately after sunrise, when ambient temperatures are low; southeast orientations experience direct sunlight during the morning as temperatures rise; southwestern orientations experience direct afternoon sun as hot afternoon temperatures decline; and northwest orientations experience direct sun immediately before sunset, when ambient temperatures have fallen. These categories, then, reflect biologically relevant physical conditions that parent birds could use in selecting a nest orientation and have been causally linked to variation in nest microclimate (Lloyd and Martin 2004).

To determine whether juncos selected nest patches that differed from locally available patches, I measured vegetative structural components associated with nest sites and randomly selected locations within 50 m of the nest site. At each nest site and random point, I laid two measuring tapes crosswise to delineate nested 5- and 11-m-radius subplots. Canopy cover from woody plants and trees >3 m was estimated by tallying the proportion of the 45 meter-marks along the tapes with target vegetation directly overhead in the 11-m-radius plot. By looking down while standing over each meter mark, I estimated groundcover as the proportion of the 45 meter-marks along the tapes with target vegetation intersecting the tape at a height of <1 m. Ground-cavity availability and orientation were estimated by systematically searching 5-m-radius plots for ground cavities that had openings 5–10 cm in diameter at their widest point and that were 10–30 cm deep, the range of dimensions of actual burrow nest sites within the study site (B. Robertson unpubl. data).

Burn severity on forest patches was defined using a modified version of the composite burn index (Key and Benson 2001). "Low-severity" patches were defined as having light charring with up to moderate consumption of litter and duff, with charring on trees being restricted to the lowest 2 m. "Intermediate-severity" patches were those with deep charring of litter and duff, increased densities of new serals (e.g., Fireweed, *Epilobium angustifolium*) compared with low-severity and unburned patches, some persistent prefire herbs and shrubs, and a few green tree crowns remaining. "High-severity" patches were characterized by largely consumed litter and duff layers, mineralized soil, and significant portions of overstory consumed, including most fine branching in crowns.

I quantified the microclimatic characteristics of each nest by measuring temperature within the nest cup continuously for 24 h

immediately after each nesting attempt. Because nest temperatures were measured before structural changes could occur to the vegetation surrounding nest sites (e.g., plant senescence), measurements of nest-site microclimate provided an unbiased index of conditions experienced by eggs, nestlings, and adults. Moreover, although nest temperatures may vary over a nesting cycle, relative nest temperature provides an unbiased method for comparing nest microclimate among nests that differ in orientation and type. I simultaneously measured ambient air temperature at a point 5 m from the nest to control for variation in ambient temperature. Nest and ambient temperatures were measured using Thermochron iButton data loggers (Maxim Integrated Products, Sunnyvale, California) placed on a plastic support stand with a rubber insulator anchored at the base of the bowl of each nest, such that the sensor was ~1 cm above the base of the nest. Although nest temperatures obtained from thermocouples are not identical to the operative environmental temperatures experienced by birds (Bakken 1992), sensors provide unbiased estimates of thermal conditions at the nest (Stoutjesdijk 2002). Ambient temperatures were measured by iButtons placed on insulated supports ~3 cm above the ground and shielded from direct sunlight with a round plastic shade 15 cm in diameter. Temperature at nests and paired ambient controls were taken at 1-min intervals for two consecutive days. Nests that were destroyed or removed by predators were excluded from analysis. Sample sizes were limited by sensor availability.

I determined whether juncos preferred to orient their nests in particular directions using a one-sample Rao's *U*-test, in which the observed distribution of directions was compared against the null hypothesis that the distribution of nest orientations was uniform (Zar 1999). To determine whether orientation changed seasonally, I used a multisample Watson-Williams test (Zar 1999). I randomly selected a suitable (see above) unused cavity from the 5-m patch surrounding each nest (if one was available) and performed a one-sample Rao's *U*-test to test the hypothesis that available ground cavities were nonrandomly oriented.

I used logistic regression to determine whether juncos preferred burrows or exposed nest sites and to compare vegetation structure at nest sites and at paired, randomly located, non-nest sites. I tested these patterns of use as a function of burn severity, percent groundcover, and postfire year, using nest initiation date as a covariate to test for seasonal changes in nest-site preference. I assessed the availability of natural cavities across seasons, burn severities, and postfire years and quantified potential differences using factorial analysis of variance (ANOVA), though the availability of exposed (noncavity) nest sites cannot be measured meaningfully at random points. Nest exposure was modeled as a function of nest orientation, nest type, and burn severity using analysis of covariance (ANCOVA) with initiation date as a covariate. I examined the relationships between nest orientation, nest type, nest concealment, and nest temperature using repeated-measures ANCOVA, with ambient air temperature included as a covariate. The maximum midday nest temperature observed at nests was modeled as a function of nest orientation, type, and concealment using ANCOVA, with mean midday ambient temperatures as a covariate. I limited the comparisons of mean nest temperatures to the hours of 1000–2000 (hereafter "midday") because direct solar radiation is likely to have little effect on nest temperature when the sun is down or low in the sky.

Nestling growth and survival.—Most nests (68% of 163) were located during nest building, egg laying, or incubation. I visited nests every day to determine the exact day of clutch completion, hatch, and fledging, and a minimum of every three or four days when these events were not imminent. I calculated nest age at the time of discovery by forward- or backward-dating of nests in relation to known dates of nest building, laying, or hatching. Nests were noted as active, successful, or failed during each visit. Active nests were those with an attending parent. Nests were considered successful if at least one young was observed as a fledgling near the nest site. Nests were considered to have failed if all eggs failed to hatch, all nestlings were found dead in the nest, or the nest was found empty before day 8 of the nestling period. Fledging occurs ~12 days after hatching (Nolan et al. 2002). Depredation was considered the cause of failure if the nest was disturbed or torn apart, eggs or nestlings were observed being eaten or removed from the nest by predators, or broken eggs or dead nestlings showed damage or injuries consistent with a predator attack. Nests were excluded from the analysis if the cause of failure was unclear or could be attributed to desertion by parents, starvation, brood parasitism, or exposure associated with extreme weather events. Assigning nest fate on the basis of static evidence at the nest (e.g., broken eggshells) introduces more bias in predation estimates than video monitoring (Etterson and Stanley 2008) but is cheaper and more logistically practical.

To estimate nestling growth rate, I individually marked nestlings immediately after hatching using a permanent marker, returning every two days to re-mark nestlings and measure body mass, length of the outermost primary on each wing (shaft, and feather when pinfeathers broke), and length of both tarsi until day 12. I used the mean of the right and left measurements for tarsus and primary length in analysis of growth rates. I estimated mass to the nearest 0.01 g using a portable electronic balance and measured primary and tarsus length to the nearest 0.1 mm using digital calipers.

Growth rates of all nestling traits were estimated by using nonlinear regression to fit a logistic growth curve to the entire data set for each trait (Ricklefs 1983, Remeš and Martin 2002). Residuals from the growth curve were pooled among nestlings within a nest before analysis (Ricklefs 1983) to avoid inflating degrees of freedom. Growth rates for each nest were represented as a single residual that reflected the average growth of nestlings (slope) in a nest in relation to all other nests in the sample. To compare growth rates of nestling traits among orientations, I analyzed pooled residuals from the nonlinear regression using multivariate analysis of covariance (MANCOVA), including brood size as a covariate (Ricklefs 1983).

I tested for variation in hatching failure and nestling mortality associated with microclimatic variation by estimating individual egg and nestling survival rates within nests using a modified Mayfield model that accounts for a lack of independence among nestlings within a nest by considering each nest as a clustered sampling unit (Flint et al. 1995). I right-censored data when nests terminated, either from fledging or failing, to focus on nestling mortality in the absence of predation pressure, and I tested for treatment effects using the program CONTRAST (Hines and Sauer 1989, Flint et al. 1995).

I examined factors affecting the daily nest predation rate (DPR, the probability that a nest will be depredated on a single

day) using the logistic exposure method developed by Shaffer (2004). Estimates were modeled using the S-shaped predictor function with the form

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

The monotonic logit link function takes the form

$$g(\theta) = \log_e \left(\frac{\theta^{\frac{1}{t}}}{1 - \theta^{\frac{1}{t}}} \right)$$

I developed a set of *a-priori* candidate models that reflected my assessment of likely causes of variation in the probability of predation on junco nests in postfire landscapes. Candidate models were built using variables that I considered potentially important in explaining variation in nest predation in postfire landscapes and variation in microclimatic variation at the nest site: (1) nest concealment, (2) severity of fire effects surrounding the nest, (3) nest orientation, (4) nest type (burrow vs. exposed), and (5) a year effect. Given the sample size of nests available for analysis and the relatively large number of models evaluated, I did not consider models with interaction terms.

I evaluated a candidate set of 15 models that I believed could reasonably explain variation in nest predation. Using PROC GENMOD (SAS institute 1999), I evaluated the degree of support for each model using goodness-of-fit tests (Hosmer and Lemeshow 1989), and Akaike's information criterion adjusted for small sample size (AIC_c ; Akaike 1973). A goodness-of-fit test of the global model (the model containing all variables) was performed to determine whether this model provided an adequate fit to the data. I determined the best model on the basis of its degree of support as indicated by ΔAIC_c and normalized Akaike weights. Models with $\Delta AIC_c \leq 2$ were considered to have substantial support, whereas models with $\Delta AIC_c \geq 4$ were considered to have little to no empirical support (Burnham and Anderson 2001). I present model-averaged DPRs by varying explanatory variables of interest while holding other variables at fixed values. Estimates are presented with their 95% confidence intervals (CIs). I used $\alpha = 0.05$ as the level of statistical significance for all hypothesis tests.

Effect of microclimate on parental behavior.—I examined how female nest attentiveness (percentage of time that females incubated) and parental feeding rate varied in response to microclimate. By monitoring feeding and incubation behavior at all nests during the same developmental stage, I controlled for natural variation in incubation and feeding that could occur during the nesting cycle. On day three of the incubation period (day last egg laid = 0), an ibutton was placed beneath the lining of each nest, equidistant from the base and rim of the nest bowl. Thermocouples recorded temperature every minute, and I inferred incubation patterns from temperature patterns in thermocouples (Lloyd and Martin 2004), thus estimating total nest attentiveness. To control for differences in weather among nests at the time of observation, I recorded ambient air temperature during foraging observations and incubation monitoring. Ambient temperature was recorded with a shaded temperature probe attached to a data logger and placed 5 m from the nest. To examine how parents responded to

changes in microclimate, I compared percentage of time spent incubating among treatments using ANCOVA, with ambient temperature and clutch size as covariates.

During two 30-min observation periods, using binoculars from a blind placed >75 m from the nest site, I quantified nestling feeding rates during the late nesting period (day 7 of the nestling period). Observations were made between 900 and 1000 hours, when neither parent was brooding young. The number of chick feeds per chick per hour was estimated for each nest, beginning immediately after the first feeding to reduce bias resulting from unequal disturbance caused by observers. I used ANCOVA to test for differences in parental allocation of food to young among nest types and nest orientations while controlling for year; Julian date and nest concealment were included in the model as covariates. Unless specifically noted, variable interactions were not considered and models were simplified until a final model containing only significant variables was achieved.

RESULTS

Habitat structure.—Successional patterns in herbaceous groundcover were an interacting function of date, postfire year, and burn severity (year \times severity: $F = 5.66$, $df = 2$ and 317 , $P = 0.004$; year \times date: $F = 14.91$, $df = 2$ and 317 , $P < 0.001$). Herbaceous groundcover was a declining function of burn severity during the first postfire year but increased to become similar among burn severities during the second postfire year (Fig. 1). Herbaceous groundcover increased seasonally across the first postfire breeding season

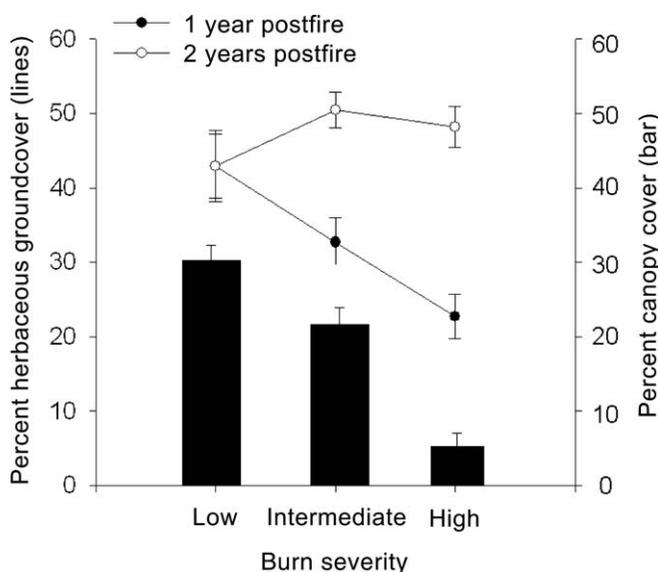


FIG. 1. Characteristics of habitat structure in the Black Mountain burn of 2003 as a function of burn severity and postfire year: estimated marginal means of percent groundcover (lines) and estimated mean percent canopy cover (\pm SE) across burn severities and two postfire years. Herbaceous groundcover was inversely related to burn severity in the first postfire year but similar across severities during the second postfire year. Canopy cover (filled bars) was inversely related to burn severity in both postfire years (yearly means pooled for presentation).

(slope \pm SE = $3.80 \pm 0.09\%$ day⁻¹) but remained relatively constant across the second postfire breeding season (-0.09 ± 0.08 day⁻¹). Canopy cover was consistently lowest in high-severity patches, whereas low-severity patches had the highest mean canopy cover (severity: $F = 76.26$, $df = 2$ and 323 , $P < 0.001$; year: $F = 2.56$, $df = 1$ and 323 , $P = 0.08$; Fig. 1).

Nest-site selection and nest temperature.—Overall, juncos preferred to orient their nests toward the north (mean = 36° , Rao's $U = 152$, $P = 0.02$, $n = 163$). Preference for north-facing nests did not change seasonally, and the distribution of nest orientation was similar when comparing early (initiated before 9 June, mean = 24.6° , $n = 99$) and late (initiated after 9 June, mean = 45.5° , $n = 64$) breeding attempts (two-sample Watson-William's test, $F = 1.24$, $df = 1$ and 162 , $P = 0.27$). There was no evidence that cavities were nonrandomly oriented in the study area (mean = 350° , Rao's $U = 132$, $P = 0.42$, $n = 135$).

Nest initiation date did not explain variation in nest types selected by females ($\chi^2 = 3.99$, $df = 1$, $P = 0.14$) and was removed from the model. The global model for the logistic regression fit the data well (Nagelkerke pseudo- $R^2 = 0.72$). Nest types selected by juncos were a function of year, burn severity, and groundcover (year: $\chi^2 = 64.16$, $df = 1$, $P < 0.001$; severity: $\chi^2 = 12.78$, $df = 2$, $P < 0.002$; percent groundcover: $\chi^2 = 74.06$, $df = 1$, $P < 0.001$). Females were more likely to place nests in burrows when vegetative cover was lower (percent groundcover: Wald $\chi^2 = 6.75$, $df = 1$, $P = 0.009$; burrow: $\bar{x} [\pm$ SE] = $34.6 \pm 5.9\%$; exposed: $\bar{x} = 47.5 \pm 3.0\%$), a condition more typical of high-severity patches (Wald $\chi^2 = 10.17$, $df = 1$, $P = 0.001$). Females were less likely to build burrow nests during the second postfire year (Wald $\chi^2 = 38.32$, $df = 1$, $P < 0.001$), when groundcover was significantly higher. These patterns were unrelated to ground burrow availability, which was consistent across years and across patches burned at different severities (both $P > 0.20$). Burrow nests were more concealed than exposed nests, but concealment did not differ in relation to fire severity or among orientations (concealment: $F = 4.22$, $df = 1$ and 156 , $P = 0.042$; severity: $F = 0.12$, $df = 2$ and 156 , $P = 0.88$; orientation: $F = 0.07$, $df = 3$ and 156 , $P = 0.97$). Nest patches did not differ from random patches in percent groundcover, litter-duff burn severity, midstory burn severity, or canopy cover (all $P > 0.30$).

Nest temperatures were recorded for 58 nests. Average nest temperatures during midday (1000–2000 hours) varied among orientations and nest types (orientation: $F = 5.01$, $df = 3$ and 52 , $P = 0.004$; nest type: $F = 7.61$, $df = 1$ and 52 , $P = 0.008$; ambient temperature: $F = 7.5$, $df = 1$ and 52 , $P = 0.01$). Nests with the preferred northerly orientations (northeast and northwest) had cooler mean temperatures than nests with southerly orientations (southeast and southwest; mean difference = 7.2°C , $P = 0.04$). Burrow nests were consistently cooler than exposed nest types (mean difference = -11.3°C , $P = 0.005$). Nest concealment did not explain significant variation in nest temperature ($P = 0.12$) and was removed from the model.

The mean maximum temperature experienced by each nest during the midday period was also related to nest orientation and nest type and was greater for less-concealed nests (orientation: $F = 4.50$, $df = 3$ and 52 , $P = 0.007$; nest type: $F = 15.25$, $df = 1$ and 52 , $P < 0.001$; concealment: $F = 6.78$, $df = 1$ and 52 , $P = 0.01$; ambient temperature: $F = 16.64$, $df = 1$ and 52 , $P < 0.001$). Exposed nest types reached higher mean maximum midday temperatures

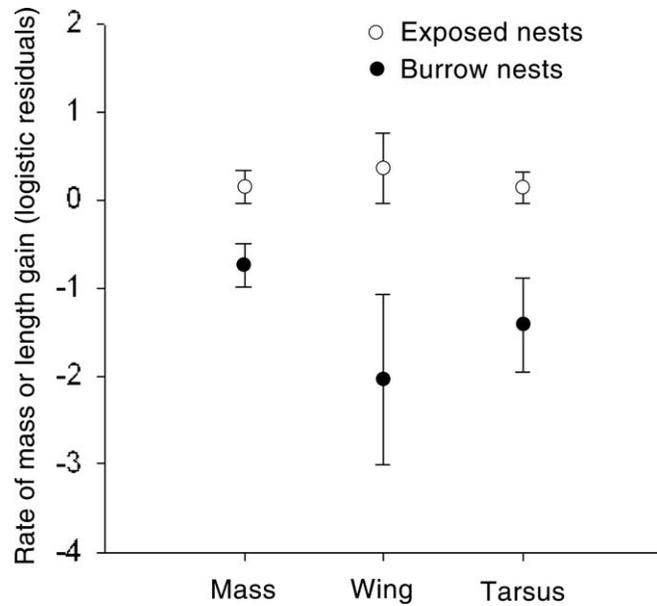


FIG. 2. Growth rate of nestling Dark-eyed Juncos as a function of nest type. Points represent the marginal means (\pm SE) of residuals from a logistic curve fit to the entire data set, averaged among nestlings within a nest and within burrow and exposed nests.

($\bar{x} = 56.2 \pm 2.8^\circ\text{C}$) than burrow nests ($\bar{x} = 40.8 \pm 4.1^\circ\text{C}$, $P < 0.001$). On average, south-facing nests reached higher maximum temperatures (southeast: $\bar{x} = 57.1 \pm 4.2^\circ\text{C}$; southwest: $\bar{x} = 59.2 \pm 4.1^\circ\text{C}$) than north-facing ones (northeast: $\bar{x} = 43.5 \pm 2.8^\circ\text{C}$; northwest: $\bar{x} = 44.4 \pm 3.4^\circ\text{C}$; mean difference = 14.1°C , $P = 0.002$). Interactions between nest orientation and nest type were nonsignificant (all $P > 0.18$) and were removed from models of nest temperature.

Ambient temperature did not differ among severities ($F = 0.64$, $df = 2$ and 48 , $P = 0.53$) and was unrelated to percent canopy cover, midstory density, and fire severity (all $P > 0.20$). Ground cover was important in reducing ambient temperatures near the ground: patches with greater proportions of bare ground reached higher maximum temperatures during midday ($F = 7.15$, $df = 1$ and 55 , $P = 0.01$).

Offspring survival and growth.—Growth rates differed between exposed and ground burrow nests (Wilks's λ , $F = 6.93$, $df = 1$ and 86 , $P = 0.01$, $n = 89$; Fig. 2). Follow-up univariate ANOVA results showed significantly lower rates of mass gain ($F = 2.71$, $df = 3$ and 86 , $P = 0.05$), wing feather growth ($F = 3.45$, $df = 3$ and 86 , $P = 0.02$), and tarsus growth ($F = 4.01$, $df = 3$ and 86 , $P = 0.02$) for young being raised in colder burrow nests (controlling for brood size; all $P < 0.03$). No measure of nestling growth was associated with nest orientation (all $P > 0.10$). Hatching date, clutch size, fledgling number, and length of the incubation and nestling periods were similar among orientations, nest types, and severities (all $P > 0.20$).

I located 163 junco nests throughout the course of the study (low-severity = 42, intermediate-severity = 59, high-severity = 62). The global model of nest predation adequately fit the data ($\chi^2 = 4.17$, $df = 8$, $P = 0.86$), and the weight of support for the best-fitting model was strong in relation to the global model (Table 1). Although five models received substantial support, only the

TABLE 1. Support for logistic exposure models predicting predation on nests of Dark-eyed Juncos in a burned landscape near Missoula, Montana, 2004–2005. Candidate models include the effects of habitat type (forest patches burned at low, intermediate, and high severity), percent nest concealment, nest initiation date, and postfire year as explanatory variables. Models were ranked using Akaike's information criterion corrected for small sample size (AIC_c). K is the number of parameters estimated by the model, $-2LL$ is $-2 \times$ the log-likelihood estimator, ΔAIC_c is the difference in AIC_c value from that of the top model, and w_i is the Akaike weight.

Model	-2LL	K	ΔAIC_c^a	w_i
Severity	168.11	2	0.00	0.84
Null ^b	166.39	1	1.36	0.42
Concealment	167.41	2	1.40	0.42
Nest type	167.35	2	1.52	0.39
Year	167.11	2	2.00	0.31
Orientation	167.00	2	2.22	0.28
Severity + orientation	167.80	3	2.74	0.21
Severity + nest type	167.30	3	3.74	0.13
Severity + concealment	167.23	3	3.88	0.12
Severity + year	167.20	3	3.94	0.12
Nest type + year	167.18	3	3.98	0.11
Orientation + year	167.11	3	4.12	0.11
Concealment + orientation	167.10	3	4.14	0.11
Concealment + year	167.01	3	4.32	0.10
Global ^c	164.10	6	16.77	0.00

^a AIC_c of the top model was 332.10.

^bNull model contains no parameters.

^cGlobal model contains all parameters.

model incorporating the effect of fire severity on DPR improved the predictive power of the null model ($\Delta AIC_c = 0.00$, $w_i = 0.84$; Table 1). Nests placed in intermediate-severity patches had a lower DPR than those in low- or high-severity patches (low-severity: 0.037, 95% CI: 0.024–0.059; intermediate-severity: 0.011, 95% CI: 0.005–0.022; high-severity: 0.036, 95% CI: 0.023–0.055). Hatching success and partial brood loss were unrelated to nest type, orientation, and burn severity (all $P > 0.70$).

Nest microclimate and parental behavior.—Females that selected southeast- or southwest-facing nests reduced their nest attentiveness during incubation, compared with females that selected northeast- or northwest-facing nests (orientation: $F = 8.29$, $df = 3$ and 83 , $P < 0.001$; nest type: $F = 0.16$, $df = 1$ and 83 , $P = 0.68$; concealment: $F = 0.094$, $df = 1$ and 83 , $P = 0.76$; Fig. 3). Burn severity and date were removed from the model because of nonsignificance (both $P > 0.52$). Parents increased their feeding rates during periods of increased ambient temperature, and adults at warmer southeast- and southwest-facing nests fed nestlings more often than parents with northerly oriented nests (mean difference = 2.3 feeds h^{-1} ; orientation: $F = 30.7$, $df = 3$ and 78 , $P < 0.001$; date: $F = 5.6$, $df = 1$ and 78 , $P = 0.02$; nest type: $F = 0.05$, $df = 1$ and 78 , $P = 0.83$; ambient temperature: $F = 7.0$, $df = 1$ and 78 , $P = 0.01$; Fig. 4). Nestling feeding rate was an increasing function of date but was unrelated to year and nest exposure (all $P > 0.2$), so these were removed from all models. Nestling feeding rates among orientations were a function of similar responses in female (orientation: $F = 4.1$, $df = 3$ and 78 , $P = 0.01$; date: $F = 4.89$, $df = 1$ and 78 , $P = 0.03$; nest type: $F = 0.97$, $df = 1$ and 78 ,

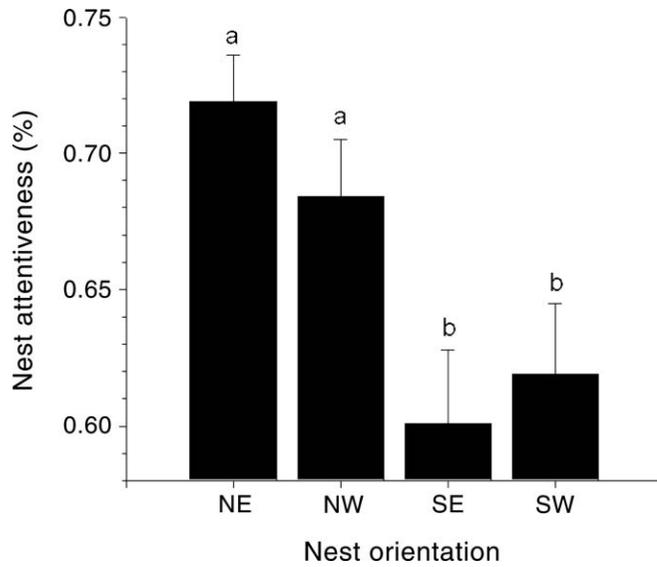


FIG. 3. Female incubation behavior of Dark-eyed Juncos as a function of nest orientation: northeast (NE), northwest (NW), southeast (SE), and southwest (SW). Data represent estimated marginal means \pm SE. Nest attentiveness (percentage of time between 1000 and 2000 hours that female sat on the nest) is greater for females incubating north-facing nests.

$P = 0.33$; ambient temperature: $F = 4.4$, $df = 1$ and 78 , $P = 0.04$; Fig. 4) and male feeding rates (orientation: $F = 6.03$, $df = 3$ and 78 , $P = 0.001$; date: $F = 4.5$, $df = 1$ and 78 , $P = 0.04$; nest type: $F = 0.10$, $df = 1$ and 78 , $P = 0.75$; ambient temperature: $F = 1.92$, $df = 1$ and 78 , $P = 0.17$; Fig. 4).

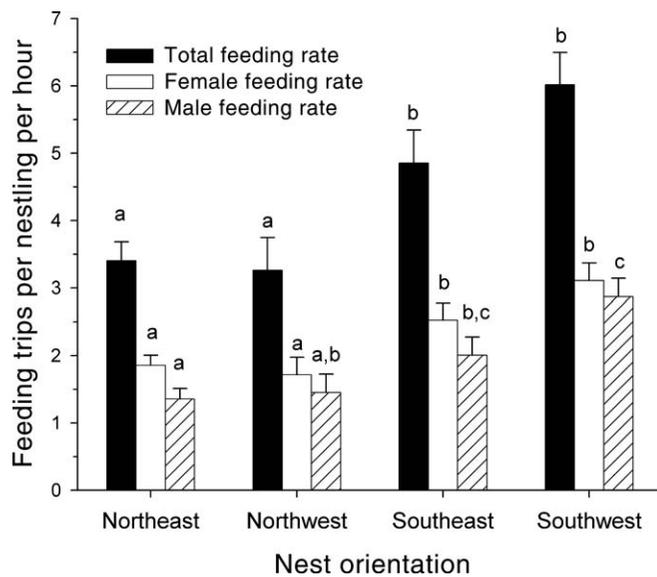


FIG. 4. Nestling feeding rates (feeding trips per chick per hour) as a function of nest orientation. Bars represent estimated marginal means \pm SE. Parents fed nestlings in south-facing nests with greatest frequency.

DISCUSSION

One of the most important choices any animal makes is where to breed, because that decision affects many of its subsequent reproductive choices (Orians and Wittenberger 1991). Natural selection should lead to the evolution of nest-site preference when there are fitness consequences associated with nest sites and a genetic basis for nest-site preference (Levins 1968). I found that Dark-eyed Juncos nesting in postfire habitats exhibited a preference for nest sites with the most moderate microclimates (exposed and north-facing). Parents selecting the warmest nest sites (exposed and south-facing) increased their feeding of young, whereas those nesting in burrows experienced slower growth rates in their offspring. Variation in nest predation was unrelated to microclimatic characteristics of nest sites, which suggests that parents do not make tradeoffs between microclimate and risk of nest predation when selecting nest sites.

Cold or hot nest microclimates should require offspring to invest more energy in thermoregulation, at a cost to the development of other traits that will affect fitness, such as body size or immunocompetence (Schew and Ricklefs 1998, Conway and Martin 2000). Experimental heating of nest cavities increased nestling growth rates in an obligate cavity-nesting species, the Tree Swallow (*Tachycineta bicolor*), which demonstrates that cold temperatures impose thermoregulatory costs on young that slow growth (Dawson et al. 2005). Variation in temperature associated with nest orientation did not affect nestling growth—as has been observed in another ground-nesting passerine, the Chestnut-collared Longspur (*Calcarius ornatus*; Lloyd and Martin 2004)—but young raised in colder burrow nests experienced retarded feather and skeletal growth and slower rates of mass gain. Alone, however, thermoregulatory costs are insufficient to explain reduced nestling growth rates in burrow nests, because nestlings raised in exposed north-facing nest sites experienced similar average temperatures with no corresponding decline in nestling growth rate. The frequency of feedings also failed to explain retarded nestling growth in burrow nests, but the quality or abundance of the food that parents conveyed to young during each visit might (these factors were not measured in the present study). In fact, burrow nests were built more frequently in high-severity patches, where food availability may have been more limited or its quality reduced.

Studies using doubly labeled water have shown that parents spend as much energy incubating as when feeding nestlings (reviewed in Williams 1996) and that metabolic costs are strongly dependent on temperature (Tinbergen and Williams 2002). High nest temperatures can increase water loss and metabolic costs to incubating parents (Haftorn and Reinertsen 1985, Dawson and O'Connor 1996), requiring more frequent forays from the nest in search of food and water (Conway and Martin 2000). As predicted, female juncos that selected hotter, south-facing nests exhibited reduced midday nest attentiveness compared with females incubating in north-facing and burrow sites that avoided direct insolation. Yet reduced attentiveness is unlikely to have resulted from hyperthermia. Birds generally maintain a body temperature of 40–42°C, and optimal incubation temperatures are in the range of 35–39°C (White and Kinney 1974, Webb 1987). Average junco nest temperatures never exceeded 34°C in south-facing sites or 25°C in north-facing sites and so are unlikely to

have caused prolonged heat-stress in incubating parents. On average, south-facing nests experienced more optimal incubation temperatures, which may have allowed attending females to spend more time on self-maintenance activities. Thermocouples do not measure the operative temperatures experienced by birds at the nest site, though it should be noted that maximum temperatures measured at nests sites significantly exceeded optimal incubation temperatures, if only for short periods of time.

Relatively higher temperatures associated with south-facing nests could also reduce the thermoregulatory costs of nestlings, freeing attending females from parental care. Evidence presented here refutes that possibility: parents with south-facing nest sites substantially increased their feeding of young with no corresponding increase in nestling growth. This is most consistent with nestlings in south-facing nests experiencing thermal stress. Lloyd and Martin (2004) found that young Chestnut-collared Longspurs reared in nests with the hottest microclimate (southeast-oriented) experienced retarded growth, a result attributed to increased shading of young by parents leading to decreased feeding of nestlings, possibly in tandem with the direct effects of high temperature. I assessed juncos' parental care behaviors on day 7, whereas Lloyd and Martin (2004) observed feeding and brooding behaviors on day 3, when altricial nestlings are still poikilothermic and unable to thermoregulate effectively (Dunn 1975). I did not measure brooding behavior, but the disparity in results between studies in parental responses to warmer temperatures in south-facing nests could be resolved if optimal parental-care strategies change in tandem with the thermoregulatory development of young. For example, shading three-day-old nestlings may be necessary to prevent mortality from hyperthermia, whereas an optimal strategy for older nestlings that can effectively thermoregulate may be to increase allocation of food and water.

Altricial nestlings thermoregulate effectively at temperatures as high as 40°C by day 7 but can withstand only relatively short periods of heat stress without becoming dehydrated (Visser 1998). Hence, although mean temperatures in south-facing nests fell within a tolerable thermal range, short-term and perhaps daily temperature spikes raising the maximum temperature at individual nest sites into the range of thermal stress may exert costs on young as their thermoregulatory ability develops to adult competence. Because parents increased their food delivery rate with increasing temperatures, use of cooler, north-facing sites also may reduce the energetic demands of parental care, especially during prolonged periods of high temperatures. Nestlings in south-facing nests may have accrued unmeasured benefits associated with more frequent feeding (e.g., increased immune function), but any increased thermoregulatory costs or water loss (or both) suffered by offspring in association with nest temperature appear to have been offset by parents (see Hoset et al. 2004).

A full explanation of juncos' nest preferences in this postfire landscape remains elusive. An apparent avoidance of cavities as breeding sites was not explained by thermal properties of nests that influenced nestling growth, hatching success, or nestling survival. Neither did parents nesting in burrows increase their nest attentiveness or nestling provisioning rates. In the early post-fire period, or in high-severity patches when the alternative is no concealment, there may be an unmeasured antipredator or thermoregulatory benefit to placing nests in cavities. Some evidence

suggests that there were thermoregulatory costs to nestlings associated with the hottest south-facing nest sites: parents increased food provisioning, but nestlings showed no corresponding increase in growth. Unpredictability in the growth and senescence of surrounding vegetation during postfire revegetation may shape nest microclimate in ways that juncos are unable to accurately predict, and nest sites that are shaded early in the nesting cycle may become more exposed as vegetation surrounding the nest shifts in structure and composition. Alternatively, females in better physiological condition may be better able to bear the thermoregulatory costs associated with hot nest sites, whereas those less able to bear such costs may be more likely to pass on thermoregulatory costs to their offspring. This hypothesis could potentially explain reduced nestling growth rates in burrow nests.

Models predicting variation in nest predation rate on the basis of the microclimatic characteristics of nest sites were poorly supported, which suggests that female juncos do not make tradeoffs between microclimate and risk of nest predation when selecting nest sites. The species responsible for most nest-predation events and their abundance and predation efficiency across fire severities remain unclear. Densities of known rodent nest predators in this region respond differently to wildfire (Stuart-Smith and Hayes 2003; Zwolak and Foresman 2007, 2008), with some preferring high-severity patches (e.g., *Peromyscus maniculatus*) and others preferring unburned patches (*Sciurus* spp.). As such, variation in the spatial distribution of nest-predator species may explain the reduced predation risk associated with intermediate-severity patches. Exposed nest sites have demonstrated advantages in allowing attending parents to detect approaching predators earlier (Götmark et al. 1995), but lack of experience and rapidly fluctuating selection may also explain observed variation in selected sites. Independent of active nest-defense behavior by parents, selection of safe nest sites may both decrease the nest encounter rate for incidental nest predators (Vickery et al. 1992) and decrease nest detectability for actively searching predators. Nest concealment did not deter nest predators in this system, which would be predicted if nonvisually oriented predators were more important.

Growing evidence suggests that conditions during nestling development influence the subsequent performance of the bird as an adult, such as its clutch size and accumulation of fat before autumn migration (reviewed in Lindström 1999). The condition of passerine birds at fledging is positively related to their probability of recruitment (Gebhardt-Henrich and Richner 1998) and yearly survival (Tinbergen and Boerlijst 1990, Gebhardt-Henrich and Richner 1998). Faster development is an advantage for offspring because it reduces the period of exposure to nest predators (Keller and van Noordwijk 1994, Martin et al. 2007). Increased energetic demands on parents during incubation are known to lead to delayed reproductive costs such as lower adult survival (Milonoff et al. 2004, de Heij et al. 2006) and depressed parental performance later in the same (Heaney and Monaghan 1996) and subsequent (Hanssen et al. 2005, Parejo and Danchin 2006) breeding attempts. Collectively, these facts suggest that the thermal regime of nest sites can have important fitness consequences for nestling and adult juncos.

Although covariation of the putative selection pressure (direct insolation) with the predicted responses in nestling growth rates and parental care strengthen inference, the correlative

nature of these results do not allow definitive conclusions about the effect of nest microclimate in shaping parental investment and nestling growth rates. Importantly, experimental manipulation of nest orientation in another ground-nesting passerine has confirmed a causal relationship between orientation and nest temperature (Lloyd and Martin 2004). South-facing nests experience hotter midday temperatures than those facing north, and the correlation between orientation and temperature is consistent across studies (Rauter et al. 2002). Even so, experimental approaches more effectively linking the microclimatic consequences of nest preference to fitness consequences are needed. Measuring microclimatic characteristics at the time nests are built by parents, rather than at the time of fledging, is preferred and is likely to more closely approximate nest preference. Wind has a less important role than solar radiation in heat balance (Wolf and Walsberg 2000, Wolf et al. 2000), and its strength is further reduced by the nature of the boundary layer of the ground (With and Webb 1993), but it may still play a role in shaping nest microclimate for ground-nesting birds.

The present study does not confirm that both temperature extremes are relevant to thermoregulation, as predicted by theory (Conway and Martin 2000), but suggests that nest microclimate can impose energetic costs on parents and offspring. Although I detected no relationship between nest-site characteristics that shaped nest microclimate and nest predation risk, other components of nest placement may serve a dual role in moderating nest temperature and reducing the risk of nest predation. Future research will benefit from considering how microclimatic costs to parents and young vary across stages of reproduction, what their long-term fitness consequences may be, and whether adult condition is an influence in the nest-selection process.

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