NEST-SITE SELECTION AND NEST SURVIVAL OF LEWIS'S WOODPECKER IN ASPEN RIPARIAN WOODLANDS

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Abstract. Riparian woodlands of aspen (*Populus tremuloides*) provide valuable breeding habitat for several cavity-nesting birds. Although anecdotal information for this habitat is available for Lewis's Woodpecker (*Melanerpes lewis*), no study has previously examined the importance of aspen woodlands to this species' breeding biology. From 2002 to 2004, we monitored 76 Lewis's Woodpecker nests in aspen riparian woodlands of south-central Idaho to describe nest-site characteristics and estimate the nests' survival. We quantified the vegetation at nest sites and randomly selected other sites to determine habitat features important in the species' selection of a nest site. We then related these features, as well as several time-specific covariates, to nest survival. Lewis's Woodpecker selected nest trees that were larger in diameter than random trees and selected nest sites with more trees, fewer woody stems, and less bare ground than random sites. However, nest-site characteristics were not important determinants of nest survival. Rather, nest-initiation date and daily maximum temperature had the strongest influence on nest survival, which was higher for early nesters and increased with increasing daily maximum temperature. Nest survival (74%) and productivity (2.3 fledglings per successful nest) were comparable to values observed for Lewis's Woodpeckers in burned pine forests, suggesting that aspen riparian woodlands also serve as valuable breeding habitat for this species in the Intermountain West.

Key words: aspen, Lewis's Woodpecker, Melanerpes lewis, *nest survival, nest-site selection,* Populus tremuloides, *riparian.*

Selección de Sitios de Anidación y Supervivencia de los Nidos de *Melanerpes lewis* en Bosques Ribereños de Álamo

Resumen. Los bosques ribereños de álamo (*Populus tremuloides*) brindan hábitat valioso de anidación para varias aves que anidan en cavidades. Aunque existe información anecdótica sobre *Melanerpes lewis* en este ambiente, ningún estudio ha examinado la importancia de los bosques de álamo para la biología reproductiva de esta especie. Entre 2002 y 2004, monitoreamos 76 nidos de *M. lewis* en los bosques ribereños de álamo en el sur-centro de Idaho, para describir las características de los sitios de anidación y estimar la supervivencia de los nidos. Cuantificamos la vegetación en los sitios de anidación y seleccionamos otros sitios al azar para determinar las características del hábitat que son importantes en la selección de un sitio de anidación por parte de la especie. Luego relacionamos estas características, junto con varias covariables temporales específicas, con la supervivencia de los nidos. Las aves seleccionaron árboles para anidar que fueron mayores en diámetro que los árboles elegidos al azar y seleccionaron sitios de anidación con más árboles, menos tallos leñosos y menos suelo desnudo que los sitios al azar. Sin embargo, las características de los sitios de anidación no fueron determinantes importantes de la supervivencia de los nidos. Más bien, la fecha de inicio y la temperatura diaria máxima tuvieron la influencia más fuerte en la supervivencia de los nidos, que fue mayor para los que se iniciaron más temprano e incrementó con los aumentos de la temperatura diaria máxima. La supervivencia de los nidos (74%) y la productividad (2.3 volantones por nido exitoso) fueron comparables con los valores observados para *M. lewis* en los bosques de pino quemados, lo que sugiere que los bosques ribereños de álamo también sirven como ambientes valiosos de anidación para esta especie en el oeste intermontano.

INTRODUCTION

Lewis's Woodpecker (*Melanerpes lewis*), a patchily distributed but often locally abundant species, breeds primarily in cottonwood (*Populus* spp.) and burned pine (*Pinus* spp.) forests throughout western North America (Tobalske 1997). This species is often termed a "burn specialist" because of its high densities and nesting success in burned forests (Bock 1970, Saab and Vierling 2001, Saab et al. 2007). Although less well documented, aspen riparian woodlands may also

provide valuable breeding habitat for this species through-out the Intermountain West. Lewis's Woodpecker has been recorded in aspen habitats anecdotally (Neel 1999, Medin and Clary 1991), but the species' use of aspen woodlands as breeding habitat has been largely unexplored. Aspen is the predominant deciduous tree at middle and higher elevations in the Intermountain West, providing the principal nesting substrate for cavity-nesting bird species throughout the region (Dobkin et al. 1995). Several studies have noted the importance of aspen as breeding habitat for cavity-nesting birds (Dobkin et al. 1995, Martin and Eadie 1999, Martin et al. 2004), and the ecological importance of this habitat is well known (Hansen et al. 2000, Campbell and Bartos 2001).

The naturally open character of aspen riparian woodlands satisfies the requirements of Lewis's Woodpecker for breeding and foraging. Unlike most woodpeckers, which bore for bark- and wood-dwelling insects, Lewis's Woodpecker is an aerial forager that requires open habitats for hawking and aerial maneuvers involved in flycatching. Additionally, a well-developed shrub layer for the production of arthropod prey and abundant perches and food-storage sites (Bock 1970, Vierling 1997) are likely important aspects of nesting habitat.

In south-central Idaho, Lewis's Woodpecker populations breeding in aspen riparian woodlands provide an opportunity for nest-site characteristics as well as nest survival in this habitat to be assessed. Identifying the habitat characteristics that influence nest-site selection and nest survival are critical to effective management. Data on nest-site characteristics and reproductive success in aspen woodlands coupled with similar information from burned pine and cottonwood habitats would provide habitat-specific demographic data needed for informed decisions for this species' management throughout its range. Land-use practices such as fire suppression, selective logging, and livestock grazing have degraded pine and cottonwood habitats throughout the range of Lewis's Woodpecker (Tobalske 1997). The loss of suitable breeding habitats has been implicated in local and regional declines of Lewis's Woodpecker populations, prompting several state and federal agencies to include this species among those of conservation concern (Neel 1999, Ritter 2000, USFWS 2008, USDA Forest Service 2009).

In this study, our objectives were to determine the habitat characteristics that influence nest-site selection of Lewis's Woodpecker in aspen riparian woodlands and to examine the influence of these characteristics on nest survival. The consequences of habitat choices determine an individual's ability to avoid nest predation and to optimize foraging opportunities to maximize reproductive success (Martin 1995, Chalfoun and Martin 2007). We expected Lewis's Woodpecker to select habitat characteristics associated with the nest site that enhance nest survival. Additionally, as an aerial forager, Lewis's Woodpecker relies upon an ephemeral and often unpredictable food source, and timing the nesting period to coincide with periods of insect emergence may be important to maximize foraging opportunities. Therefore, we also expected that the timing of nesting and weather conditions that influence insect availability, such as nest-initiation date and temperature, would also affect nest survival.

METHODS

STUDY AREA

The study area was located in Butte and Blaine counties, Idaho in the foothills of the Pioneer Mountains, north of the Snake River Plain. This portion of the state is a mix of private and public lands used primarily for cattle and sheep grazing. Elevation of the study area varies from 1600 to 2000 m, and vegetation is characteristic of the Intermountain sagebrush steppe ecosystem (West 1983). The landscape is composed of narrow riparian zones (≤50 m in width) dominated by aspen, gray alder (*Alnus incana*), willow (*Salix* spp.), mountain snowberry (*Symphoricarpos oreophilus*), and rose (*Rosa* spp.), within a matrix of sagebrush steppe (*Artemisia* spp.). Black cottonwood (*P. balsamifera*) also occurs along some streams. Stands of aspen also occur on the toes of slopes and in pockets where snowmelt accumulates at higher elevations along drainages. In these areas, aspen communities are persistent, self-perpetuating stands, and conifers are generally absent (Mueggler 1985, 1988). Such stable aspen communities persist in the absence of large-scale disturbances such as fire (Kurzel et al. 2007, Rogers et al. 2010). During the breeding season (May–August) daily temperatures range from a low of −3 °C to highs of over 38 °C, and average monthly rainfall ranges from 5 to 46 mm (weather station, Craters of the Moon National Monument, Butte County, Idaho).

Sheep and cattle graze throughout the study area. Study sites were similar with regard to timing of grazing and number of livestock. We chose four study sites, two grazed by cattle and two grazed by sheep. Each study site consisted of approximately 300–500 ha of aspen habitat.

NEST-DATA COLLECTION

We surveyed for Lewis's Woodpecker nests from mid-May to early August during three breeding seasons (2002–2004). We located nests by searching aspen riparian woodlands and discrete aspen stands for potential nest trees and cavities, observing behavior (e.g., courtship, copulation), and checking previously used nest cavities. We defined an occupied nest as a cavity containing at least one Lewis's Woodpecker egg or nestling. We monitored nests from the time they were found until the young fledged (at least one nestling left the nest) or the nest failed, visiting them every 1–6 days with the most common intervals being 2, 3, and 4 days. Intervals between visits were typically longer during incubation and the early nestling stage, but we visited nests almost daily as the young neared fledging. Additionally, we visited every nest on the first day of each stage of nesting whenever possible.

To obtain nest-initiation date, clutch size, hatch date, and number of nestlings, we viewed nest contents with a monochrome pinhole camera mounted on the end of a telescoping pole (TreeTop II; Sandpiper Technologies, Inc.). We were able to view the contents of all cavities ≤13 m in height except in rare cases when this was prohibited by the angle of the cavity or dense vegetation. We viewed nest contents at every nest visit during laying to determine the onset of incubation but typically viewed them only once or twice through the incubation and nestling periods. We defined initiation date as the date the female laid the first egg of the clutch and the onset of incubation as the date the female laid the final egg of the clutch. To reduce the risk of forcing nestlings to fledge prematurely, we did not view nest contents when nestlings were within 10 days of fledging. During visits when we did not view nest contents, we evaluated the status of the nest by observing parental behavior from a point ≥15 m from the nest tree.

We confirmed fledging by observing fledglings on or near the nest tree. Lewis's Woodpecker fledglings occasionally reenter the nest cavity and typically remain in the vicinity of the nest for several days after fledging (K. Newlon, pers. obs.). We considered a nest to have failed if the cavity contained dead nestlings or the nest was empty before the earliest possible date of fledging.

HABITAT MEASUREMENTS

At each nest, we established an 11.3-m-radius circular plot with a nested 5-m-radius circular subplot centered on the nest tree. Methods and plot design follow Martin et al. (1997) and Saab et al. (2009) with some modifications. For each 11.3-m plot, we recorded the number of live trees and snags (standing dead trees) >1.37 m in height and ≥20 cm in diameter and measured the following characteristics: tree species, diameter at breast height (dbh), and tree height. Within the 5-m subplot, we measured the density of woody stems by counting all woody stems between 0.5 and 1.37 m in height and estimated bare ground by a point-intercept method. We placed a sharpened dowel every 0.5 m from the center of the plot in four

perpendicular directions for a total of 40 measurements. We totaled the number of times the dowel hit bare ground out of 40 measurements and converted this to a percentage of bare ground. For each nest tree, we measured its dbh, condition (live or dead), and height and the nest cavity's height. We also recorded the cavity's orientation and the slope and slope aspect at each cavity tree.

We characterized potentially available nest sites by establishing 60 random points placed at least 200 m apart throughout aspen riparian habitat, using the Random Point Generator (Jenness 2005) in ArcView 3.3 (ESRI 2000). Plots established at random points had the same design as those established for nest plots. To compare nest trees' characteristics, we randomly chose a tree available for nesting from each random 11.3-m-radius plot. Lewis's Woodpecker did not nest in trees <21 cm in diameter, so we considered any tree (live or dead) ≥20 cm in diameter as available for nesting. For each randomly selected tree, we took the same measurements as at the nest tree, except those specific to the nest cavity. Because non-nest plots were selected randomly, they did not necessarily contain a tree suitable for nesting.

STATISTICAL ANALYSES

Nest-site selection. We used logistic regression to determine the habitat variables that influenced nest-site selection. We developed a list of a priori candidate models that allowed us to model the odds that a tree contained a Lewis's Woodpecker nest as a function of several covariates based on biological hypotheses from published literature. We incorporated five continuous habitat variables into the set of candidate models and a categorical grazing-treatment variable to assess the influence of cattle and sheep grazing on nesting habitat (Table 1).

We evaluated support for the candidate models with an information-theoretic approach (Burnham and Anderson 2002), comparing by Akaike's information criterion corrected for small sample size (AIC_c). We ranked models by their ΔAIC_c values (the difference in AIC_c value between each candidate model and the model with the lowest AIC_c value) and Akaike

TABLE 1.   Variables incorporated into candidate models determining habitat variables that influence nest-site selection by Lewis's Woodpeckers nesting in aspen riparian woodlands in south-central Idaho, 2002–2004.

Variable	Hypothesis
Tree height	Taller trees allow for higher nests that are less accessible to tree-climbing nest predators.
Diameter at breast height	Larger diameter trees provide warmer and more stable temperatures in the nest cavity.
Woody-stem density	Higher stem densities provide more substrates for arthropod prey.
Tree density	Higher tree densities provide more sites for perching and food storage.
Percent bare ground	Increased percentage of bare ground increases visibility of prey to woodpeckers foraging on the ground.
Livestock grazing (cattle vs. sheep)	Incorporated as a categorical variable to assess the influence of cattle and sheep grazing on nesting habitat.

TABLE 2.   Candidate models and supporting hypotheses for survival of Lewis's Woodpecker nests in aspen riparian woodlands in south-central Idaho, 2002–2004.

Models	Variables	Hypotheses
Null	Intercept only	Nest survival is random; assumes daily survival rate is constant.
Temporal, environmental effects	Nest-initiation date, maximum daily temperature, precipitation, year, nest age	Early nesters will have higher nest survival. Higher temperatures and lower precipitation increase nest survival by creating favorable environmental conditions and increasing options for foraging. Annual variation in food and predators affects nest survival. Nest age influences nest survival by influencing the behavior of nestlings and adults.
Nest-site characteristics	Nest height, nest-tree diameter at breast height, woody-stem density, tree density, percent bare ground	Factors associated with nest survival will be consistent with those associated with nest-site selection. Physical features associated with the nest site provide greater protection from predators and increase availability and visibility of prey.
Grazing-treatment effect	Categorical treatment variable	Cattle and sheep have different preferences in foraging, resulting in different effects on vegetation.

weights (w_i; a measure of support for the model). We estimated the overdispersion parameter ($\hat{c}$) of our global model with the goodness-of-fit test of Hosmer and Lemeshow (2000).

We computed adjusted odds ratios and their confidence limits (95% profile likelihood) for our top model with PROC LOGISTIC (SAS Institute 2000). Adjusted odds ratios allowed us to evaluate the magnitude of the effect of each predictor variable while holding all other variables constant. We interpreted an adjusted odds ratio for a continuous predictor variable as the odds of a tree containing a Lewis's Woodpecker nest for every n-unit increase in the continuous variable. We chose the unit of increase on the basis of values of the variable that we believed would be biologically significant and meaningful to managers. We interpreted adjusted odds for the categorical treatment variable as the odds of one category relative to another (i.e., cattle-grazed vs. sheep-grazed). Note that 95% confidence limits around an adjusted odds ratio that overlap 1 indicate that particular covariate had effectively no influence on nest-site selection.

Nest survival. We modeled estimates of daily survival rate (DSR), the probability of a nest surviving a single day, by using a generalized linear-models approach (PROC NLMIXED; SAS Institute 2000) with a logit link that constrained the estimates of DSR between 0 and 1 (Agresti 1996). This procedure allowed us to model (1) the binomially distributed data as a function of several nest- and time-specific continuous or categorical covariates, (2) nonlinear relationships between covariates and DSR, and (3) covariates that varied in a predictable manner, such as nest age. We set confidence limits on nest-survival estimates by using the delta method (Seber 1982). We used ΔAIC_c to rank our models and w_i to evaluate the support for each model, given our data. Analysis methods are detailed in Dinsmore et al. (2002) and Rotella et al. (2004, 2007). To evaluate the models' fit, we used a goodness-of-fit test based on an unweighted sum of squares of the models' kernel-smoothed residuals developed by Sturdivant et al. (2007).

We developed a set of models based on a priori biological hypotheses to explain variation in nest survival of Lewis's Woodpecker (Table 2). Additionally, we incorporated an observer-effect variable into the best-supported model to determine if viewing nest contents had an impact on DSR. Viewing nest contents may influence nest survival (either positively or negatively), resulting in potentially biased estimates of DSR (Rotella et al. 2000). The incorporation of this observer effect allowed DSR to vary for days that nest contents were viewed. This effect was coded as an indicator variable where 1 = contents viewed, 0 = contents not viewed. For this analysis, we assumed that viewing nest contents affected DSR only on the day nest contents were viewed.

RESULTS

NESTS

We found 76 Lewis's Woodpecker nests during the breeding seasons of 2002–2004. The number of nests found as well as the proportion of successful nests varied annually (Table 3). For all years combined, the distance to the nearest Lewis's Woodpecker nest averaged 349 m ± 477 (SD; range 0–3207 m). We found 56 nests on cattle-grazed sites and 20 nests on sheep-grazed sites. Overall, 59 nests fledged at least one young. Of the 17 nest failures, 13 were caused by predation.

We found 45 nests before (i.e., when adults were modifying cavities) or during egg laying, 16 nests during incubation, and 13 nests during the nestling stage. The average length of the nesting cycle for successful Lewis's Woodpecker nests in the study area was 51 days ± 3 (range 45–61 days). In 2003, clutches averaged larger, the number of fledglings averaged more, initiation averaged earlier, and dates of hatching and fledging averaged later than in either 2002 or 2004 (Table 3). Clutch size declined with later date of initiation in the breeding season. Average clutch size in nests initiated before 4 June was 6.5 eggs ± 1.2 (n = 15 nests), between 4 June and 15 June

TABLE 3.   Number of nests monitored, average dates of nest initiation, hatching, and fledging, and average clutch size and number of fledglings per successful nest for Lewis's Woodpecker nests in south-central Idaho, 2002–2004. Means are followed by 1 SD (n, range). SD of dates of nest initiation, hatching, and fledging is expressed in days.

Year	Number of nests monitored	Clutch size	Initiation date	Hatch date	Fledge date	Fledglings per successful nest
2002	18	5.7 ± 1.0	8 June ± 9	24 June ± 8	24 July ± 1	2.0 ± 1.0
		(6, 4 − 7)	(23 May–25 June)	(11 June–9 July)	(13 July–31 July)	(14, 1–4)
2003	33	6.2 ± 1.2	3 June ± 6	21 June ± 5	23 July ± 1	2.4 ± 0.9
		(25, 5 − 9)	(23 May–15 June)	(10 June–2 July)	(13 July–3 August)	(30, 1–5)
2004	25	5.3 ± 1.2	10 June ± 7	28 June ± 7	28 July ± 1	2.3 ± 0.5
		(21, 3 − 8)	(1 June–25 June)	(21 June–11 July)	(19 July–5 August)	(15, 2–3)
Overall	76	5.8 ± 1.2	7 June ± 8	24 June ± 7	25 July ± 1	2.3 ± 0.9

it was 5.8 eggs ± 1.0 (n = 26 nests), and after 15 June it was 4.9 eggs ± 1.1 (n = 11 nests). The majority of nests (58%) were initiated on or before 6 June, and over the entire study nest-initiation dates ranged from 23 May to 26 June. For this study, we considered 23 May the first day of the breeding season.

HABITAT MEASUREMENTS

Mean values (± 1 SD) of habitat characteristics at Lewis's Woodpecker nests were highly variable (nest height: 6.5 m ± 3.4; nest-tree dbh: 41.3 cm ± 15.3; number of trees per hectare: 225 ± 150; number of stems per hectare: 3050 ± 3050; bare ground: 11.7% ± 11.7). Five of the 76 Lewis's Woodpecker nests monitored for nest survival were located just outside the study area in locations where we did not establish random points, so we used 71 nests in our analysis of nest-site selection. Two nests were placed in natural cavities in black cottonwood; the remaining 69 nests were in aspen. Fifty-seven of the 76 nests were located in live aspen. The majority (54%) of nest trees contained more than one cavity. The woodpeckers reused 14 nest trees; ten nest trees were used twice, and four nest trees were used three times during the study.

We did not know if the same birds were reusing nest cavities they had used in previous breeding seasons because birds were not individually marked. As we were interested in the odds that a tree contained a Lewis's Woodpecker nest, given our set of covariates, we included all 71 nests in our analysis. Nine of the 60 random plots did not contain a tree suitable for nesting, so we incorporated 51 random plots into our analysis of nest-site selection.

Density curves reveal that nest trees were larger in diameter than trees measured at random plots, and nest plots had more trees, fewer woody stems, and less bare ground than did random plots (Fig. 1). We do not provide a density curve for tree height because tree heights in nest and non-nest plots were similar. Additionally, only 18 of 76 nests had a measurable slope, so we did not consider slope and aspect in further analyses. Habitat characteristics at sites grazed by cattle and those grazed by sheep were similar.

FACTORS INFLUENCING NEST-SITE SELECTION

The global model adequately fit the data (χ^2_8 = 9.1, P = 0.3) and received all of the support (AIC_c = 109.51, Akaike weight = 1.0, model likelihood = 1.0). The next closest model was 15.79 ΔAIC_c units greater than the best-supported model. The woodpeckers' nest-site selection was positively influenced by dbh and tree density and negatively influenced by increasing amounts of bare ground and woody stems (Table 4). The odds of a tree containing a Lewis's Woodpecker nest doubled with every 5-cm increase in diameter, and the odds of a plot containing a Lewis's Woodpecker nest increased by 28% with the addition of one tree. Conversely, the odds of a plot containing a Lewis's Woodpecker nest decreased by 27% with the addition of 50 woody stems. With every 5% increase in bare ground, the odds of a plot containing a Lewis's Woodpecker nest decreased by 24%. Tree height was not a good predictor of whether or not a tree contained a nest. Incorporation of a treatment effect revealed that nests were 11.3 times more likely to occur on cattle-grazed sites than on sheep-grazed sites.

FACTORS INFLUENCING NEST SURVIVAL

Results from the goodness-of-fit test indicated the global model fit the data (P = 0.21). In the model that assumed a constant DSR, nest survival was 0.9941^{51} = 0.74 (95% CL = 0.63, 0.85). However, this model was not well supported (Table 5), indicating that the addition of covariates better explained variation in DSR of Lewis's Woodpecker nests. The model that received the most support given our data indicated that DSR was negatively related to nest-initiation date ($\hat{\beta}$ = −0.18 ± 0.04; 95% CL = −0.25, −0.11) and positively related to daily maximum temperature ($\hat{\beta}$ = 0.19 ± 0.06; 95% CL = 0.07, 0.31). The logistic regression equation for our best model was logit (DSR) = 3.44 − 0.18(initiation date) + 0.19(daily maximum temperature).

The model incorporating precipitation, initiation date, and daily maximum temperature also received support. Precipitation had a negative influence on DSR, but the parameter estimate was highly imprecise ($\hat{\beta}$ = −6.01 ± 4.96; 95% CL −15.74, 3.73).
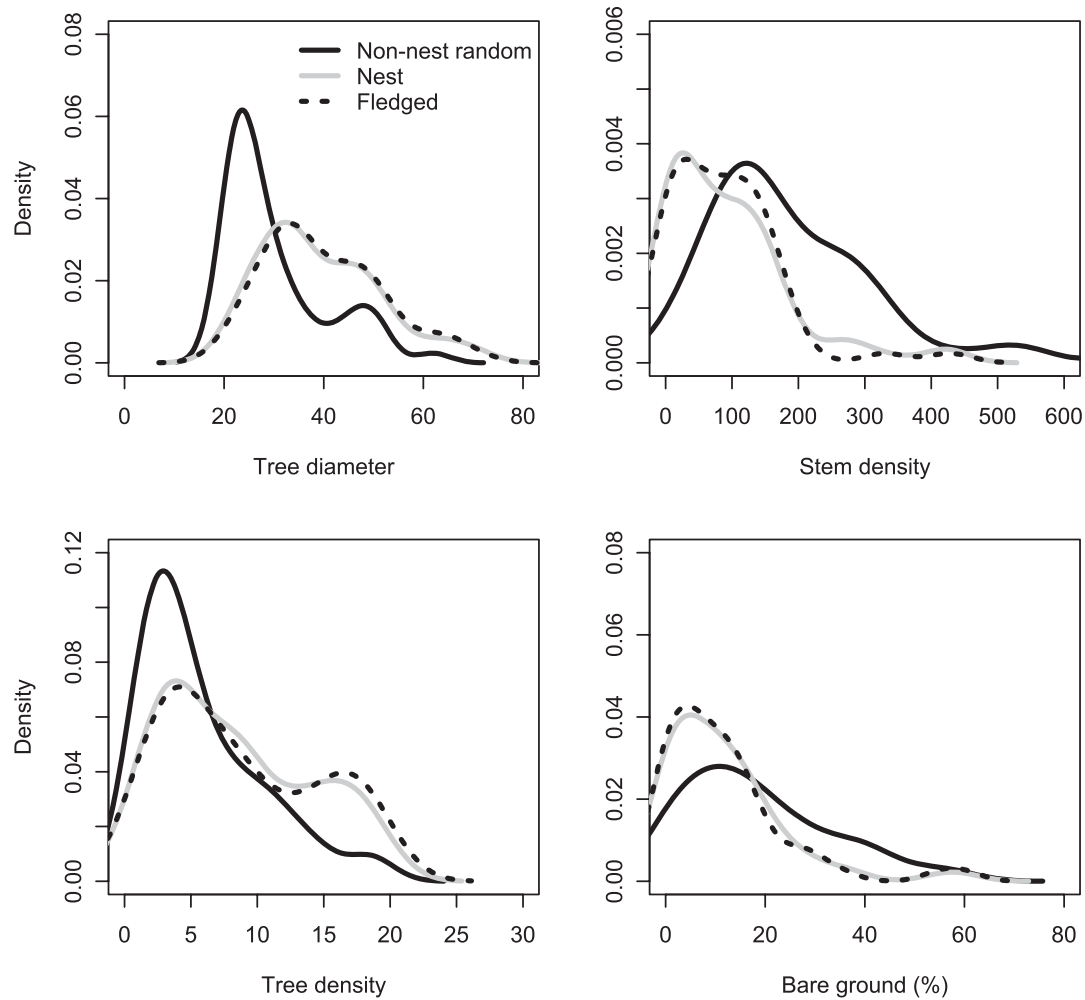
FIGURE 1.   Density curves for habitat characteristics measured at randomly selected non-nest sites ($n = 51$), nest sites ($n = 76$), and nests that successfully fledged at least one young ($n = 59$).

TABLE 4.   Parameter estimates (±SE) and adjusted odds ratios from the best model for predicting nest-site selection by Lewis's Woodpecker nesting in aspen riparian woodlands in south-central Idaho, 2002–2004. The odds ratio for the categorical variable grazing treatment indicates the odds of a nest site being selected in a cattle-grazed vs. a sheep-grazed site. Odds ratios for continuous variables indicate the odds of a site containing a nest for every unit change (specified in the "units" column) in the variable. Confidence limits that do not contain 1 represent a difference in the odds.

		Adjusted odds ratio		
Parameter	Parameter estimate ± 1 SE	Unit	Estimate	95% profile likelihood confidence limits
Intercept	−4.00 ± 1.32			
Dbh (cm)	0.14 ± 0.04	5	2.06	1.49, 3.08
Tree height (m)	−0.07 ± 0.07	1	0.93	0.81, 1.05
Number of trees	0.25 ± 0.07	1	1.28	1.14, 1.48
Number of woody stems	−0.01 ± 0.01	50	0.73	0.57, 0.90
Bare ground (%)	−0.05 ± 0.02	5	0.76	0.62, 0.92
Grazing treatment	1.21 ± 0.32	1	11.25	3.47, 43.88

TABLE 5.   Selection results for the candidate models explaining variation in daily survival rate of Lewis's Woodpeckers nesting in aspen riparian woodlands in south-central Idaho, 2002–2004. Models are ranked from most supported ($\Delta AIC_c = 0$) to least supported; K is the number of parameters in each model. The Akaike weight (w_i) is the weight of the evidence for model i, given the data. The model likelihood indicates the support of the model, given the data.

Candidate model	K	ΔAIC_c [a]	w_i	Model likelihood
Initiation date + daily maximum temperature	3	0.00	0.58	1.00
Initiation date + daily maximum temperature + precipitation	4	0.87	0.37	0.65
Nest age + initiation date	3	5.60	0.04	0.06
Initiation date	2	7.62	0.01	0.02
Nest age	2	18.23	0.00	0.00
Year (2002 + 2004)	3	23.41	0.00	0.00
Constant daily survival rate	1	27.10	0.00	0.00
Precipitation	2	27.12	0.00	0.00
Grazing treatment	2	27.82	0.00	0.00
Diameter at breast height + nest height	3	28.69	0.00	0.00
Stem density + tree density + bare ground + grazing treatment	5	31.53	0.00	0.00
Stem density + tree density + bare ground	4	31.57	0.00	0.00

[a] The AIC_c value for the top model was 153.18.

Although the model incorporating year as a covariate did not receive strong support, the influence of both the 2002 and 2004 breeding seasons on DSR was negative ($\hat{\beta}_{2000} = -1.37 \pm 0.78$; 95% CL −2.87, 0.13, $\hat{\beta}_{2004} = -1.63 \pm 0.67$; 95% CL = −2.94, −0.32) relative to that of the 2003 breeding season. Models including habitat characteristics at the nest site and grazing treatment received no support, and all confidence limits for the coefficients included zero.

The addition of an observer effect to the best model indicated that viewing nest contents had a strong negative effect on DSR for those days on which we viewed nest contents ($\hat{\beta} = -2.12 \pm 0.58$; 95% CL = −3.27, −0.98). The parameter estimates for initiation date ($\hat{\beta} = -0.16 \pm 0.04$; 95% CL = −0.23, −0.09) and daily maximum temperature ($\hat{\beta} = 0.14 \pm 0.06$; 95% CL = 0.01, 0.26) changed slightly with the addition of this variable.

To evaluate the effects of initiation date and daily maximum temperature on the daily survival of Lewis's Woodpecker nests, we plotted DSR as a function of nest-initiation date and daily maximum temperature for nests initiated early (29 May) and late (16 June; Fig. 2). Nests initiated earlier in the season had consistently higher daily survival rates regardless of daily maximum temperature.

DISCUSSION

Although several studies have examined characteristics of Lewis's Woodpecker's nest sites, no study has investigated the influence of these characteristics on nest survival. We found that Lewis's Woodpecker nest sites differed from random non-nest sites by having more trees, fewer woody stems, and less bare ground. Additionally, nest trees were larger than other available trees. Yet none of the nest-site features that we measured influenced nest survival. Instead, nest survival was most influenced by trends associated with nest-initiation date and daily maximum temperature. A complex interaction of environmental variables, food availability, and nest predators likely influences habitat choices, reproductive effort, and nest survival (Zanette et al. 2006, Chalfoun and Martin 2007, Drever and Clark 2007).

NEST-SITE SELECTION

In aspen riparian woodlands, characteristics of Lewis's Woodpecker nest sites are consistent with those in burned pine and riparian cottonwood habitats (Vierling 1997, Gentry and Vierling 2008, Saab et al. 2009), suggesting that Lewis's
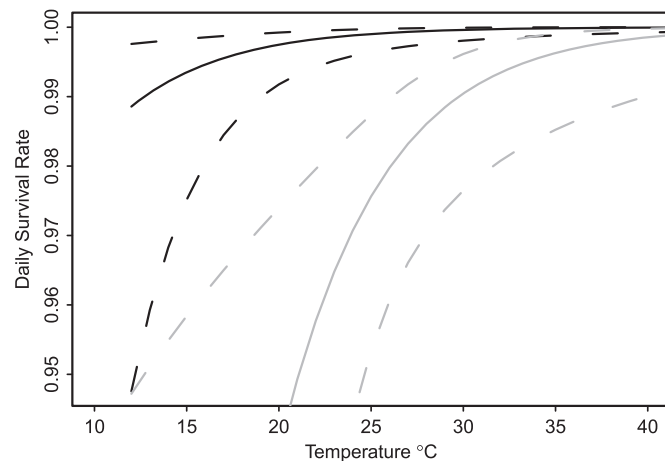

FIGURE 2.   Estimated daily survival rate (DSR) and 95% confidence intervals of Lewis's Woodpecker nests as a function of increasing daily maximum temperature for nests initiated early (29 May; in black) and late (16 June; in gray) in the nesting season.

Woodpecker selects similar nest-site attributes irrespective of habitat. A shrubby understory has been assumed to be an important attribute of the species' breeding habitat because it is associated with an increase in arthropod prey (Bock 1970, Tobalske 1997, Saab and Vierling 2001), yet we found that an increase in the density of woody stems was not associated with nest sites. The abundance of woody stems at the nest tree may have less influence on foraging than does the abundance of woody stems in the surrounding landscape. Indeed, Lewis's Woodpecker likely selects characteristics associated with foraging and nesting habitat at different spatial scales, as broad-scale variables such as climate and edaphic patterns may dictate food availability (Rotenberry and Wiens 1991, 1998, Chalfoun and Martin 2007).

In burned pine and cottonwood riparian habitats, Lewis's Woodpecker nests are located almost exclusively in dead or dying trees (Bock 1970, Saab and Vierling 2001, Gentry and Vierling 2008). Decayed trees provide the soft wood on which many woodpecker species rely to facilitate cavity excavation. In this study, the majority of Lewis's Woodpecker nests we located were in live trees. The importance of live aspen infected with heartrot fungus has been noted for many cavity nesters (Harestad and Keisker 1989, Dobkin et al. 1995, Martin et al. 2004), and the susceptibility of aspen to heartrot fungus creates ideal conditions for cavity excavation (Hart and Hart 2001, Aitken et al. 2002). As a result, aspen habitats typically support high breeding densities of woodpeckers (Dobkin et al. 1995, Martin et al. 2004). High densities of excavators and the cavities they create in response to these conditions may provide abundant nest sites for Lewis's Woodpecker in aspen riparian woodlands.

We cannot explain why Lewis's Woodpecker placed nearly four times more nests in cattle-grazed sites than in sheep-grazed sites, as the vegetation characteristics we measured were similar in both. Yet other factors, such as vegetation structure and plant-species composition, may have differed, subsequently influencing arthropod diversity and abundance (Dennis et al. 1998, Brose 2003). Vegetation structure and composition are affected by not only the act of grazing but also by a complex relationship of the rates and schedules on which the animals are stocked and rotated (Knopf et al. 1988, Saab et al. 1995). The indirect effects of livestock grazing on arthropod numbers and their subsequent influence on food availability for birds merit further study. Moreover, examination of nest-site characteristics at additional spatial scales would provide further insight into the processes influencing Lewis's Woodpecker's selection of nest sites.

NEST SURVIVAL

Unexpectedly, nest survival was not influenced by habitat characteristics important for nest-site selection. Patterns of habitat use are presumed to have evolved in response to fitness consequences (Orians and Wittenberger 1991, Martin 1998,

Robertson 2009). Habitat choices influence the ability of an individual to acquire food (Rotenberry and Wiens 1988) or escape predators (Martin 1998). These habitat choices can, in turn, influence components of fitness such as reproductive effort. Although the influences of habitat choices on fitness consequences vary with spatial scale (Chalfoun and Martin 2007), an individual's ability to assess its potential fitness within a particular habitat is essential to its survival and productivity (Citta and Lindberg 2007).

Of the variables that we incorporated into our models, nest-initiation date had the strongest influence on nest survival, and nests that initiated earlier were more likely to succeed. Although early nesters risked colder temperatures, this risk apparently did not exceed the overall benefits of nesting early. The positive influence of early nest initiation on reproductive success has been reported for several species of birds (Bryant 1988, Brown and Brown 1999, Blums et al. 2002), but the mechanism driving this relationship is unclear.

One hypothesis is that differences in nest-initiation date reflect differences among individual birds. For example, individuals in good condition can initiate nesting earlier and have higher reproductive output, whereas birds in poorer condition must delay nesting until they reach adequate condition, typically laying fewer eggs (Perrins 1970). Although a direct relationship between clutch size and nest survival is not well founded in cavity-nesting birds (Martin 1993a) and is inconclusive in both passerines (Lima 2009) and waterfowl (Drever and Clark 2007), we did see a relationship between nest-initiation date and clutch size. In our study, early nesters had the largest clutches, and clutch size declined with later nest initiation, suggesting that early nesters may have been in better condition. Nest-initiation dates may also vary with the bird's age, as older, more experienced individuals tend to initiate nesting earlier (Sæther 1990, Blums et al. 2002). Although we do not know the ages of the Lewis's Woodpeckers we studied, nests in cavities the birds used the previous breeding season were initiated earliest, suggesting that older birds may have been returning to and reusing these nest sites.

A second hypothesis is that nest initiation is dictated by environmental variables such as temperature and precipitation. Several studies have noted the influence of environmental variables on reproductive success (Conway and Martin 2000, Drever and Clark 2007, Stodola et al. 2010). Specifically, birds may synchronize nesting with periods of high food abundance, which in turn is influenced by these environmental variables (Lack 1966). Indeed, Bock (1970) observed annual variations in timing of Lewis's Woodpecker's breeding in relation to weather conditions in California, and we observed a similar pattern, suggesting that synchronization of nesting with periods of insect emergence may be an important contributor to nest survival. Variation in the earliest and mean initiation dates among the three breeding seasons of our

study suggests birds may have varied the onset of breeding in response to environmental variables that influenced prey availability. Lewis's Woodpecker concentrates its foraging on temporarily abundant prey, exploiting abundant food resources when it matters most (Bock 1970).

Although we collected valuable demographic data by using a cavity viewer, incorporating an observer effect into our nest-survival models (Rotella et al. 2000) suggested a substantial negative influence on DSR for those days on which we viewed nest contents. Our viewing a cavity may have cued potential predators to a nest or resulted in reduced nest attendance by adults. Excluding this covariate from our models would have resulted in negatively biased estimates of DSR, yet including it allowed us to examine the survival rate of nests for days unaffected by viewing of nest contents. For example, adding an observer effect to our null model, which assumes a constant DSR, increased our overall nest-survival estimate from 0.74 (95% CL = 0.63, 0.85) to 0.88 (95% CL = 0.78, 0.97) for days that we did not view nest contents. Given that we typically viewed the contents of any one nest fewer than four times during the nesting cycle, the effect on overall nest survival in this study may have been minor. Nevertheless, we encourage others to consider any potentially negative consequences and weigh these with the overall benefits this tool provides in answering their research questions.

VALUE OF ASPEN AS BREEDING HABITAT

The values of overall nest survival for Lewis's Woodpecker breeding in aspen riparian woodlands are similar to those reported for burned pine habitats (Saab et al. 2007) and nearly twice those reported for cottonwood riparian habitats (Saab and Vierling 2001). Saab and Vierling (2001) hypothesized that the disparity in reproductive success between burned pine and cottonwood riparian habitats results from differences in the assemblages and abundances of predators. We observed potential nest predators such as the Long-tailed Weasel (*Mustela frenata*) and Least Chipmunk (*Tamias minimus*) in the study area frequently, yet overall survival rates for Lewis's Woodpecker nests remained high. Aspen woodlands often have an abundance of cavities, resulting in increased densities of suitable nest sites that could decrease the probability of a predator locating an individual nest (Martin 1993b). We propose that an abundance of cavities in aspen riparian woodlands may have decreased the chance of a predator discovering a Lewis's Woodpecker nest. Moreover, the majority of Lewis's Woodpecker nest trees contained multiple cavities, perhaps further reducing the risk of predation. The situation in recently burned forests may be similar, as these postfire habitats attract high densities of primary-cavity-nesting birds (Saab et al. 2005, 2007). The high predation rates Saab and Vierling (2001) observed in cottonwood riparian habitats may have been related to reduced cavity abundance, as all Lewis's Woodpecker nests located in that study were in natural cavities (Vierling 1997), suggesting that cavities excavated by woodpeckers were limited or absent. If cavity abundance were in fact reduced, then the likelihood of predators finding a cavity occupied by a Lewis's Woodpecker nest would increase. Examining the relationship between excavators, cavity abundance, and predation rates of Lewis's Woodpecker nests across habitats would provide valuable insights into the mechanisms driving nest predation.

The high values of nest survival and productivity we observed for Lewis's Woodpecker suggest that aspen riparian woodlands provide high-quality breeding habitat for this species in the Intermountain West. We encourage further study of Lewis's Woodpecker in aspen woodlands. Moreover, increased monitoring in aspen riparian woodlands may provide a better indication of the status of Lewis's Woodpecker populations because of the stability of these habitats relative to ephemeral postfire forests. Additionally, information is needed on reproductive success in riparian woodlands that are not grazed by livestock. Although Breeding Bird Survey data suggest Lewis's Woodpecker populations are declining at a rate of 1.2% per year (Sauer et al. 2008), this species' sporadic distribution and the known detection biases associated with the Breeding Bird Survey increase the difficulty of assessing its population status and emphasize the need for habitat-specific studies. Reductions in burned pine and riparian cottonwood habitats, the species' primary breeding habitats, have been implicated in declines of Lewis's Woodpecker populations (Tobalske 1997). Fire suppression and loss of large trees to logging have reduced the availability of suitable burned pine habitats (Allen et al. 2002). Additional losses in nesting habitat have resulted from the absence of cottonwood regeneration and seedling establishment in riparian woodlands due to dams, water diversions, and livestock grazing (Saab et al. 1995, Scott et al. 1997, Rumble and Gobeille 2004).

Aspen constitutes a small proportion of the landscape in western North America, yet it supports some of the highest diversity of flora and fauna (Hansen et al. 2000). Although the aspen stands we studied appear to be regenerating successfully (Newlon, unpubl. data), and aspen stands in other regions of the western U.S. are persisting (Kashian et al. 2007, Kurzel et al. 2007), some aspen stands have declined as a result of several factors including heavy browsing by both domestic and wild ungulates (Mueggler 1989, Kay 1997, Hessl 2002). Aspen stands are diverse in their modes of regeneration, ecological gradients, and genetics. As a result, the status of aspen across large areas of the western U.S. cannot be generalized without regard for the stands' complex local dynamics (Kashian et al. 2007, Kurzel et al. 2007, Rogers et al. 2010). The dynamic nature of aspen stands and the spatial variability in drivers of their characteristics further emphasize the need for a regionwide assessment of aspen woodlands as breeding habitat for Lewis's Woodpecker.

ACKNOWLEDGMENTS

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