Lewis's Woodpecker nest success and habitat selection in floodplain and burned forests in western Montana

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ABSTRACT. For species with declining populations across their range, such as Lewis's Woodpeckers (*Melanerpes lewis*), understanding habitat selection and its influence on reproductive outcomes are critical for effective management, especially in human-modified landscapes. We identified factors associated with habitat selection by Lewis's Woodpeckers in the floodplain and burned forests across the Bitterroot Valley in Montana. We estimated population densities, determined reproductive outcomes, and examined the possible influence of forest characteristics on nest-site selection. Mean adult population densities of Lewis's Woodpeckers were over three times greater in floodplain forest than burned forest (13.2 adults/km^2 vs. 4.1 adults/km^2, respectively). However, nest success was lower in floodplain (73%; CI = 62%, 82%) than in burned forest (88%; CI = 78%, 94%). Nest success also declined across the breeding season. Lewis's Woodpeckers in the floodplain forest were more likely to nest in cavities in taller trees, forested areas with reduced canopy cover, and stands with more trees. In burned forests, the height of nest trees was the only distinguishing feature of nest-site selection. However, the characteristics of nest sites used by Lewis's Woodpeckers did not predict nest success. Ultimately, nest success was high in both forest types and both play an important role in maintaining populations of Lewis's Woodpeckers in our study system. Management strategies to conserve habitat for Lewis's Woodpeckers in western Montana should focus on retention of trees and snags > 18 m in height in both forest types, as well as enhancing recruitment of cottonwoods in a floodplain forest.

RESUMEN. **Éxito reproductivo y selección de hábitat en *Melanerpes lewisi* en bosques inundables e incendiados en el oeste de Montana**
Para especies con poblaciones en disminución a través de su rango de distribución, como es el caso de *Melanerpes lewisi*, entender la selección de hábitat y su influencia sobre el éxito reproductivo es crucial para el manejo efectivo, especialmente en paisajes transformados por los humanos. Identificamos los factores asociados con la selección de hábitat por *Melanerpes lewisi* en bosques incendiados e inundables a lo largo del valle de Bitterroot en Montana. Estimamos la densidad poblacional, determinamos el éxito reproductivo y examinamos la posible influencia de las características del bosque sobre la selección de los sitios de anidación. La densidad promedio de la población adulta de *Melanerpes lewisi* fue mas de tres veces mayor en los bosques inundables que en los bosques incendiados (13.2 adultos/km^2 vs. 4.1 adultos/km^2 respectivamente). Sin embargo, el éxito de los nidos fue menor en los bosques inundables (73%; CI = 62%. 82%) que en los incendiados (88%, CI= 78%, 94%). El éxito reproductivo también disminuyo a lo largo de la temporada de reproducción. En los bosques inundables, *Melanerpes lewisi* anidó con mayor probabilidad en cavidades de arboles más altos, áreas con bosque con cobertura de dosel reducida y áreas con una mayor cantidad de árboles. En los bosques quemados, la altura de los arboles utilizados para anidación fue la única característica particular de la selección del sitio de anidación. Sin embargo, las características de los sitios de anidación utilizado por *Melanerpes lewisi* no predijo el éxito reproductivo. En última instancia, el éxito del nido fue alto en ambos tipos de bosques y los dos bosques juegan un papel importante en el mantenimiento de las poblaciones de *Melanerpes lewisi* en nuestro sistema de estudio. Las estrategias de manejo para conservar el hábitat para *Melanerpes lewisi* en el oeste de Montana deben enfocarse en la retención de arboles y tocones > 18 m de altura en ambos tipos de bosque, así como promover el reclutamiento de Álamos en los bosques inundables.

Key words: cottonwood forest, ecological trap, nest-site selection, population density, reproductive outcomes, species of concern

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Habitat selection influences the demography of populations and is integral for effective conservation planning (Rosenzweig 1981, Martin 1992). Adaptive habitat selection

arises when organisms select a habitat that conveys the highest fitness (e.g., reproductive success or survival; Fretwell 1972, Cody 1985, Martin 1998). However, habitat selection may not always be adaptive, especially in modified landscapes. Some individuals may select habitat types with low survival rates or reproductive success, leading to low population growth and even population sinks where population growth (λ) is negative (Arlt and Pärt 2007, Chalfoun and Schmidt 2012). To unravel how habitat influences population trajectories, one approach is to compare population densities with reproductive outcomes across different habitat types. First, population densities across the commonly used habitat types need to be measured to understand habitat preferences. Second, careful analysis of reproductive outcomes or survival in these habitat types is crucial for characterizing the influence of habitat selection on population trajectories (Van Horne 1983). Linking the availability of preferred habitat characteristics to where species populations are successful may allow better management and conservation of species of concern.

Information about population densities and reproductive rates may provide insight to support management decisions (Jones 2001). Estimates of population densities are key because they provide a baseline appreciation for habitat preferences. Reproductive rates inform the demographic consequences of these choices (Pulliam 1988, Martin 1992, 1998). Individual reproductive success measures an individual's ability to rear at least one young each year and factors into population growth (Pulliam 1988). Other reproductive parameters such as brood or clutch sizes, attrition (i.e., loss of young), and overall productivity also contribute to population growth and can vary independently from reproductive success (Pettifor et al. 2001). However, these demographic rates are often examined in isolation so comparing reproductive rates with population densities across different habitat types may provide more insight into mechanisms driving population change.

Closer analysis of environmental factors across habitats may reveal other factors contributing to low reproductive rates and low productivity (Martin 1992, 1998, Chalfoun and Schmidt 2012). Recent studies of habitat selection and reproductive outcomes in various bird species have demonstrated that nest-site selection can be associated with low nest success and negative growth rates in parts of species' ranges (Donovan et al. 1995, Robinson et al. 1995, Arlt and Pärt 2007, Chalfoun and Martin 2007). Species with declining populations that are reliant on human-altered landscapes may be especially subject to habitat selection that results in low reproductive success (Chalfoun and Martin 2007). Hence, careful examination of the relationship between population density and reproductive outcomes, as well as specific habitat features across habitat types is needed, especially for species of conservation concern.

Lewis's Woodpeckers (*Melanerpes lewis*) are secondary-cavity nesting birds that occur throughout western North America, but with populations declining across their range (Sauer et al. 2014, Vierling et al. 2020). Populations have declined since 1960, with accentuated declines in the Northern Rockies region (Sauer et al. 2014). Limited knowledge of the drivers behind these declines has led to concerns over their conservation status in Montana, USA (Montana Field Guide 2021), and Canada (ECCC 2017).

Lewis's Woodpeckers nest across a diversity of forest types, but most commonly in riparian lowland forests, burned conifer forests, and pine forests (Bock 1970, Macfarland et al. 2019, Vierling et al. 2020). The influence of nest-site selection and macrohabitat type on their reproductive success is still unclear (Saab and Vierling 2001, Saab et al. 2009, Zhu et al. 2012, Macfarland et al. 2019, Vierling et al. 2020). Nest success (46%) in a cottonwood forest in Colorado was thought to reflect the presence of an ecological trap (Saab and Vierling 2001). However, nest success in cottonwood floodplain forests in British Columbia, Canada, was reasonably high (69%; Macfarland et al. 2019), raising questions about the importance of this forest type for Lewis's Woodpeckers. Similarly, nest success in a burned conifer forest in British Columbia was low (15%; Macfarland et al. 2019), but higher in mixed-conifer forests that burned 2–25 years previously (i.e., 78–90%; Linder 1994, Saab and Vierling 2001, Gentry and Vierling 2007, Saab et al. 2007, Vierling et al. 2009). In short, the relative importance of floodplain and burned forests for populations of Lewis's Woodpeckers

remains unclear. However, few studies of Lewis's Woodpeckers in floodplain forests have been conducted (Saab and Vierling 2001, Fylling 2013, Macfarland et al. 2019). Moreover, the relative contribution to populations also depends on relative population densities among these habitats, but estimates of population densities are lacking across these forest types.

We report population densities and reproductive outcomes of Lewis's Woodpeckers in the floodplain and burned forests. Our study sites in the Bitterroot Valley, Montana, appear to have the highest reported densities of breeding Lewis's Woodpeckers in Montana (MASCR 2016, eBird 2021). The ubiquitous presence of nesting habitat in the Bitterroot Valley provides an exemplary study system for identifying drivers of density and reproductive success across two commonly used habitat types at risk of human perturbation.

METHODS

Our study was conducted in the Bitterroot Valley (Fig. 1) of southwestern Montana during the full nesting cycle of Lewis's Woodpeckers from May to August 2015 to 2017. We focused our research on the extensive floodplain and burned conifer forests commonly used by Lewis's Woodpeckers (Fylling 2013) and avoided other forest types with few or no Lewis's Woodpeckers based on preliminary roadside surveys in 2014 across our study area.

Floodplain forests along the Bitterroot River were characterized by lower montane riparian woodlands and shrublands dominated by black cottonwood (*Populus balsamifera* ssp. *trichocarpa*), and variable amounts of Ponderosa pine (*Pinus ponderosa*). This plant community occurred on relatively flat valley bottoms, but sometimes directly abutted steep hills and mountains. Most floodplain forests in our study were privately owned, except for several state and federal owned parcels, including the Lee Metcalf National Wildlife Refuge.

Burned forests belonged to the Rocky Mountain Ponderosa Pine woodland and savanna type (MF Guide 2018), dominated by Douglas-fir (*Pseudotsuga menziesii*), Ponderosa pine, small amounts of western larch (*Larix occidentalis*), and lodgepole pine (*Pinus*

contorta latifolia). Common deciduous shrubs included alder (*Alnus* spp.), red-osier dogwood (*Cornus stolonifera*), willows (*Salix* spp.), and thimbleberry (*Rubus parviflorum*). Burned forests occurred on mountain slopes and steep hills, with small creeks often occurring at the base of drainages. We only used areas under 2300 m in elevation because we found no evidence of breeding above that elevation during several roadside surveys in 2014. Most of the burned forest was on public land managed by the Bitterroot and Lolo National Forests. Within areas identified as floodplain or burned forest, we selected two types of sites for different analytical purposes: randomized point locations throughout the valley to examine population densities, and non-randomized field sites to monitor nests and measure breeding and nest-site characteristics.

Population density. We conducted Bitterroot Valley-wide surveys to estimate the abundance of adult Lewis's Woodpeckers and calculate population densities in the floodplain and burned forests in 2016 and 2017. We mapped the distribution and occurrence of floodplain and burned forest layers in the Bitterroot Valley using ArcGIS (ESRI 2011). We generated random points to conduct 60 point counts in each forest type per year for a total of 240 surveys across the study period. We defined floodplain forests as those within both the 100-yr flood zone and within 1 km of the Bitterroot River high watermark (USFS 2014). We included burned forests that were 5–18 years post-fire to encompass most fire histories found important to Lewis's Woodpeckers in other studies (Saab and Vierling 2001, Saab et al. 2007, 2009). We were not able to access burned forests 1–4 years post-fire, despite their known importance to Lewis's Woodpeckers for colonization and high nest success (Saab et al. 2007, 2009). Our use of random points allowed us to capture the range of fire severity, intensity, fire extent, and post-fire regeneration.

Nest monitoring. We monitored nests of Lewis's Woodpeckers, assessed breeding productivity, and measured associated vegetation and habitat characteristics at four floodplains and five burned forest sites during the 2015–2017 breeding seasons. We selected sites using several criteria, including accessibility (e.g., much floodplain forest is privately
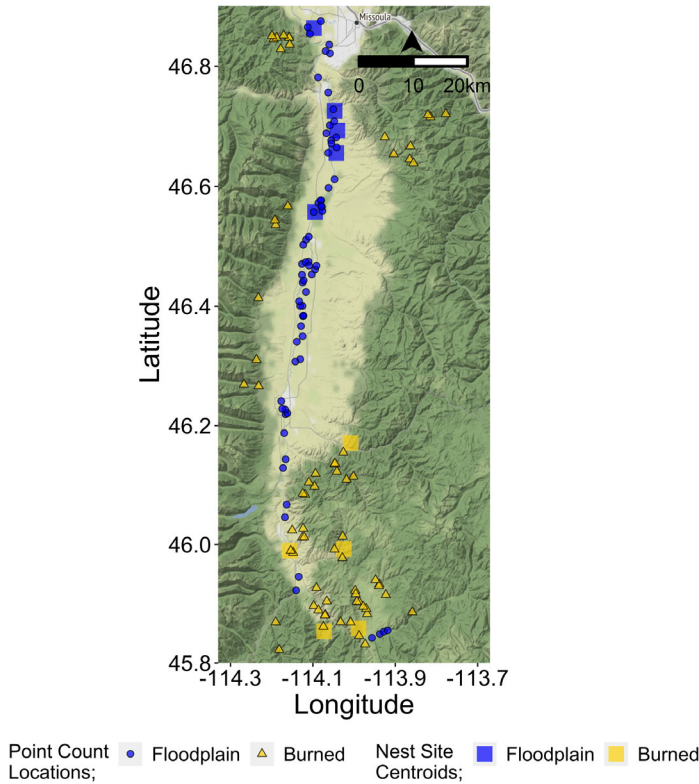
Fig. 1. Map of our study area showing the nest-monitoring field site centroids, and point count locations in the floodplain and burned forests in the Bitterroot Valley, Montana.

owned), forest area (i.e., sites that could accommodate large enough samples of nests), and pre-established Lewis's Woodpecker research (i.e., on-going nest-monitoring and color-banding projects). Field sites ranged in size from 0.21 to 6.31 km². At burned sites, fire severity was moderate to high (Richardson 2001) and often resulted in stand-replacement conditions. Burned forest sites were all within the perimeter of the Skalkaho Fire, a large (212,000 ha) wildfire that occurred in 2000. This burned forest complex was the most widely available burned habitat in the Bitterroot Valley at the time of our nest-monitoring efforts, and selecting all nest-monitoring sites at the same postfire age and intensity allowed us to compare nests in one burned forest type. Additionally, the Skalkaho Fire provided an opportunity to monitor a burned forest older (i.e., 15–18 years postfire) than those in most previous studies (i.e., 2–15 years since the fire; Saab et al. 2007,

2009, Macfarland et al. 2019, Vierling et al. 2020). Burned forests are known to be important for nesting by Lewis's Woodpeckers until at least 22 years post-fire (Bock 1970, Vierling et al. 2020). We searched for nests using a combination of systematic and opportunistic searches, using both visual and audio cues such as territorial flights over nest trees, known territorial or aggressive vocalizations (e.g., male "churr" call), observation of woodpecker pairs investigating cavities, or copulation. At each field site, our main nest-searching efforts occurred early in the field season (May–June). However, we continued to search for nests throughout the season when we heard or saw individual Lewis's Woodpeckers away from known nest trees or if we observed a nest failure in case adults renested nearby.

Vegetation plots for nest-site selection. At each field site, we collected data on the cavity and nest-tree characteristics, as

well as features of the surrounding forest. We characterized the forest surrounding nest trees by centering an 11.3-m sampling plot around nest trees (Li and Martin 1991, Martin et al. 1997). We paired this nest plot with up-to-two additional random plots to sample available, but unused, nesting sites in the same forest type (Martin 1998). We set all random plots at random distances from nests and in a systematic direction. Random plots were located from 20 to 250 m from nest plots. In floodplain forest, random plots were systematically downstream and parallel to the Bitterroot River, or the farthest direction allowed from the Bitterroot River. In the burned forest, random plots were downslope in the drainage or at the same elevation gradient of nest plots. We attempted to sample two random plots when space was available, but were not always able to find adequate forest habitat (e.g., limited by private land or development projects). To establish the center of each random plot, we selected the closest snag or partially dead tree suitable to cavity-nesting woodpeckers, but not currently in use (e.g., dbh > 23 cm; Saab and Vierling 2001, Saab et al. 2009), and with at least one cavity with an entrance of > 4 cm in diameter.

Population density. Point counts were conducted in early July during the early and middle nestling stage to maximize detectability of adults because they are constantly foraging and delivering food to nests, and to reduce chances of counting fledged young later in the season. We conducted 10-min point counts using visual (i.e., foraging adults above treetops or perching on tree snags) and auditory cues (i.e., adult flight, alarm, and territorial calls, and male churrs; Bock 1970). We recorded time and distance for all detections (Amundson et al. 2014). Based on our previous work, using playback to detect Lewis's Woodpeckers was unreliable. Visual displays are the most prevalent indicator of nesting behavior, and territorial vocalizations are given for only a short period of time. Lewis's Woodpeckers are loudest and most visually obvious during direct challenges by conspecifics on or near nest trees (e.g., chatter calls accompanied by display behavior). In our study area, these interactions often occurred 30 m above the forest floor and call-back surveys at ground level would not approximate normal conditions. We also did

not want to attract woodpeckers from great distances, potentially biasing our count results.

We estimated population density by calculating the mean number of Lewis's Woodpeckers per point count location relative to the detectable area at each point count (i.e., maximum radius fixed at 500 m, or 0.79 km^2 per count). We modeled the mean number of Lewis's Woodpeckers at point counts across the two forest types using a hierarchical distance-sampling and time-removal N-mixture model in a Bayesian framework following the methods of Amundson et al. (2014) and Kéry and Royle (2015). This allowed us to assess the effect of countbiases inherent to imperfect detection during fieldwork. Specifically, we accounted for two detection biases: availability (i.e., probability that Lewis's Woodpeckers are present and available to be counted during point counts) and perceptibility (i.e., probability of detecting Lewis's Woodpeckers when available during point counts; Amundson et al. 2014, Kéry and Royle 2015). We set availability as equal between forest types, but allowed perceptibility to vary between the floodplain and burned forest because of the difference in vegetation structure between forest types. We implemented the Bayesian models in JAGS (Plummer 2003) using the R package "jagsUI" (Kellner 2021). For the effect of habitat type on detection and abundance, we specified diffuse normal prior distributions with mean 0 and variance 100. Example model code is provided in Amundson et al.'s (2014) supplemental code. We ran four Markov Chain Monte Carlo chains of 15,000 iterations each and retained 2500 values per chain, after discarding 5000 for adaptation and burn-in and thinning by four. We conducted all analyses in RStudio (RStudio Team 2020) using R-4.0.2 core software (R Core Team 2020).

Nest-site selection. We estimated the Resource Selection Functions (RSF) using logistic regression to approximate a used-availability model (Johnson et al. 2006, Lele et al. 2013, McDonald 2013, Fierro-Calderón and Martin 2020, Millspaugh et al. 2020). We compared used nest-site characteristics from the nest plots collected during our vegetation surveys and available nest plots that did not include an active nest, but had

at least one cavity in a snag or tree with a suitable diameter at breast height (dbh). We compared characteristics of the nest plots between used and available nest trees in an RSF framework with a binary outcome (used or available; Manly et al. 2002, McDonald 2013, Fierro-Calderón and Martin 2020).

Nest-tree and nest-area characteristics. We measured nest-tree height (m), nest-tree dbh (cm), nest-tree health (dead or alive), heart rot (present or absent; floodplain forest only), and burned class (burned forest only). We also included the presence of branches touching a nest tree to model the potential effect that branches provide access to nest trees to predators (e.g., squirrels and chipmunks), which may influence woodpecker nest-site selection. In each sampling plot, we recorded aspect (four categorical groups based on compass heading; burned forest only), slope (percent, burned forest only), average canopy cover (percent; floodplain forest only), average shrub height (m), number of live trees (floodplain only), and number of snags.

Nest-site selection analysis. We conducted separate Generalized Linear Model (GLM) analyses to determine nest-site selection within each forest type. We developed a list of a priori candidate models in two variable sets corresponding to nest-tree characteristics and nest-area covariates. Nest-tree characteristics included nest height (m), nest-tree height (m; floodplain sites only), dbh (cm), the presence of heart rot (no/yes; floodplain only), nest cardinal orientation (four categorical groups based on compass heading), average shrub height (m), and whether the nest tree was dead or alive (0.1; in floodplain sites only). Nest-area covariates included canopy cover (percent cover; floodplain only), number of living trees (floodplain only), number of snags, slope (burned sites only), and aspect (burned sites only; four categorical groups based on compass heading). We first modeled these variable sets separately. We tested all covariates for multicollinearity and all variables were centered and scaled with mean zero and standard deviation equal to one. We fit logistic regression functions and used the base R glm functions to run the RSF models, and "MuMIn" package (Bartón 2020) to automate the model selection. We conducted model selection using Akaike's Information Criterion corrected for small sample sizes

(AIC_c) and ranked models based on the smallest delta AIC_c (Burnham and Anderson 2001). We then carried forward the predictors from the top model of each variable set and conducted a final combined analysis (Table 1A).

Nest monitoring. We rotationally surveyed field sites every 1–4 days and monitored all nests at each site following established nest-monitoring protocols (Martin and Geupel 1993). We measured nest success, clutch size, and attrition rates (an index of nest productivity, see below) for all active nests (i.e., at least one egg laid) we could access. We considered nests successful if at least one young fledged (Martin and Geupel 1993).

Nest success. We estimated daily survival rates (DSR) using the logistic exposure method (Shaffer 2004). We calculated DSR using a GLM framework to test the effects of multiple covariates based on biological hypotheses related to nest success. We modeled DSR at floodplain and burned sites separately to include unique factors related to each forest type. As with nest-site selection, we used a hierarchical model selection approach to compare suites of explanatory variables. We modeled DSR as a function of the year, day of the year, nest-tree characteristics, and nest-area measures (Tables S3–S5). Model selection was based on AIC_c, and ranking models based on the smallest delta AIC_c (Burnham and Anderson 2001). We then carried forward the predictors from the top model of each variable set and conducted a final combined analysis (Table 1B).

To assess nest success from the start of incubation to fledge date, we used the top model from our model selection and exponentiated the mean DSR value for each forest type by the average nesting period duration in days (Shaffer 2004, Powell 2007). We approximated variance and reported 95% confidence intervals of nest success estimates using the delta method following Powell (2007).

Attrition analysis. We also calculated attrition, i.e., the number of young lost between egg-laying and nestling stages. This calculation provides a metric of reproductive effort versus productivity that might illuminate the environmental stressors affecting the outcome. We calculated attrition from successful nests

Table 1. Final model selection of (A) nest-site selection by Lewis's Woodpeckers and (B) nest-success analyses in floodplain and burned forests.

	k	LL	ΔAIC_c	*wi*
A. Nest-site selection				
Floodplain				
Nest tree height[Nt] + canopy cover[Na] + tree count[Na]	4	−77.61	0.00	0.89
Canopy cover[Na] + tree count[Na]	3	−80.81	4.27	0.11
Nest tree height[Nt]	2	−85.35	11.23	0.00
Null (intercept)	1	−87.15	12.79	0.00
Burned				
Nest tree height[Nt]	2	−67.06	0.00	0.99
Null (intercept)	1	−72.66	9.12	0.01

	k	LL	ΔAIC_c	*wi*
B. Nest success				
Floodplain				
Canopy cover[Na] + hatch day[T]	3	−77.36	0.00	0.45
Hatch day[T]	2	−78.99	1.14	0.25
Canopy cover[Na]	2	−79.32	1.81	0.18
Null (intercept)	1	−80.79	2.67	0.12
Burned				
Hatch day[T]	2	−38.86	0.00	0.98
Null (intercept)	1	−43.64	7.46	0.02

(A) Models are ranked by the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c) and we also display the calculated model's Akaike weight (w_i), and Log-Likelihood ratio (LL) for additional comparisons of our ranked models. The top model for nest-site selection in floodplain forest is $AIC_c = 163.55$. The top model for nest-site selection in the burned forest is $AIC_c = 138.24$.
(B) The top model for nest success in floodplain forest is $AIC_c = 160.94$. The top model for nest success in the burned forest is $AIC_c = 81.86$.

as one minus the number of young that fledged divided by the number of eggs laid in a nest. We assumed attrition to be normally distributed across our study area. We conducted a studentized *t*-test between the floodplain and burned forests to evaluate the difference in attrition levels. Values are presented as means ± 1 SD, unless otherwise specified.

RESULTS

Population density. The density of Lewis's Woodpeckers was more than three times greater in floodplain forest (13.2 [95% CI = 9.9, 18.2] adults/km^2) than in burned forest (4.1 [95% CI = 2.7, 6.2] adults/km^2; Fig. 2A). These estimates accounted for separate measures of perceptibility and availability on detection biases. Perceptibility was significantly higher in burned than floodplain forests (Fig. 2B). Time-removal analysis revealed that $72 \pm 7\%$ of the breeding population of Lewis's Woodpeckers at each site was present during our point count sampling efforts (detection bias of availability across our study system).

Nest-site selection. We monitored 258 Lewis's Woodpecker nests, including 150 in floodplain and 108 in burned forest. Due to the availability of covariate information collected at each nest, we were only able to include 204 for our analysis of nest success (115 in floodplain and 89 in burned), and 233 for nest-site selection (128 in floodplain and 105 in burned).

When assessing nest-site selection, we analyzed final models from two variable sets in each forest type: nest-tree characteristics and nest-area characteristics. For the nest-tree analysis, the only characteristic retained was nest-tree height in both forest types (Table S1). In our nest-area analysis, we found support for canopy cover and tree count in floodplain forests (Table S2). We found no support for any nest-area variables in predicting nest-site selection in the burned forest; the null model with no predictors was the top-performing model (Table S2). Variables from each top-performing model in each variable set were carried forward to a final model selection using multimodal inference to assess relative model support for each forest type (Table 1A). The final model comparisons of nest-site selection in floodplain forest indicated effects of nest-tree height, canopy cover, and tree count on nest-site selection (based on the top model with all covariates > 2 ΔAIC_c from the second model; Table 1A). Only nest-tree height was retained and included in the final top model for nest-site selection in the burned forest (Table 1A).

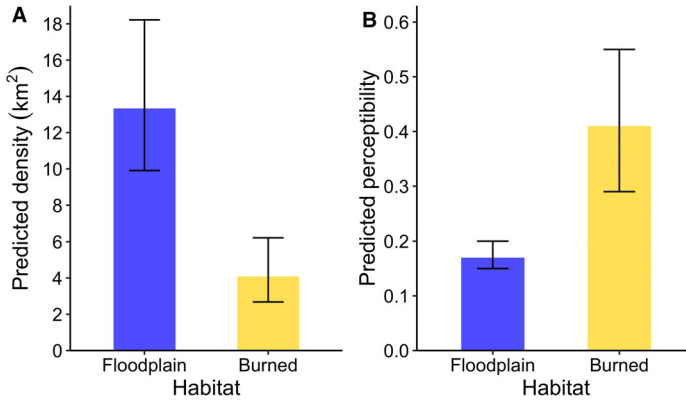Nest-tree height and tree count had a positive effect on nest-site selection, whereas

Fig. 2. Mean predicted density estimates for Lewis's Woodpeckers per forest type (A) and mean perceptibility probabilities of detecting Lewis's Woodpeckers per forest type (B), calculated using the mean abundance estimates per point count. Error bars represent 95% credible intervals of the estimates.

canopy cover had a negative effect (Table 2 A). The effect of nest-tree height on nest-site selection was positive in both floodplain and burned forest (Table 2A, Fig. 3). Lewis's Woodpeckers nested in different species and sizes of trees in the two forest types ($t_{120} = 2.5$, $P = 0.015$), nesting in cotton-wood trees (73.0 ± 19.1 cm dbh) in flood-plain forest and ponderosa pine snags (66.2 ± 17.2 cm dbh) in burned forests. Nest-tree height averaged 20.8 ± 6.4 m in the floodplain and 18.5 ± 7.5 m in the burned forest. Canopy cover averaged $55 \pm 28\%$ in floodplain forest, but we were unable to detect significant cover at nest trees in the burned forest. The density of suitable trees and snags for Lewis's Woodpeckers (i.e., dbh > 23 cm; Saab and Vierling 2001) was greater, but more variable, in the floodplain (132 ± 100 stems per hectare) than burned forest (60 ± 43 stems per hectare).

Breeding productivity. *Nest success.* We found little support for either nest-tree or nest-area variables predicting nest success in either forest type (Tables S3 and S4). In floodplain forest, the top-performing model included only canopy cover. Our modeling efforts retained no nest-tree or nest-area variables for the burned forest. We did find temporal factors important in both forest types; hatch date was included in the top model for both floodplain and burned forests (Table S5). Variables from each top-performing model in each variable set were carried forward in a final model competition (Table 1

B). After combining temporal, nest-tree, and nest-area variable sets, models from the final model comparison for nest success in the floodplain were within 2 ΔAIC_c, although the top model included both canopy cover and hatch date (Table 1B). The effect of canopy cover on nest success in the floodplain was positive, but not significant (Table 2B). The effect of hatch date was larger than the effect of canopy cover and negative, indicating a decline in nest success across the breeding season in floodplain forest (Table 2B, Fig. 4A). Only hatch date was retained in the final model comparison for nest success in the burned forest (Table 2B). The negative effect of hatch date on nest success was twice as strong in burned as in floodplain forest (Table 2B, Fig. 4A).

After controlling for mean hatch date, we found high nest success in both forest types, although lower in the floodplain (73%, CI = 62%, 82%) than burned forest (88%, CI = 78%, 94%). Hatch dates differed ($t = -3.9$, $P < 0.001$) between forest types, with a mean hatch date of 18 June in the floodplain and 22 June in the burned forest; hatch dates varied considerably in both forest types (Fig. 4 B). The mean duration of nesting periods from egg-laying to fledging was 45.8 ± 3.3 days.

Clutch size and attrition. Clutch size averaged 6.0 ± 1.5 eggs ($N = 93$) and did not differ between floodplain and burned forests ($t = 1.5$, $P = 0.13$). Clutch size in each habitat decreased during the breeding season

Table 2. Final model coefficients for the top model covariates retained in (A) nest-site selection by Lewis's Woodpeckers and (B) success analyses. Superscripts indicate the variable set the individual explanatory variables belong to, including Nt – nest tree, Na – nest area, and T – temporal.

	Effect (CI)	*P* value
(A) Nest-site selection		
Floodplain		
Intercept	0.37 (0.00, 0.74)	
Nest tree height^{Nt}	0.50 (0.11, 0.89)	0.01
Canopy cover^{Na}	−0.81 (−1.26, −0.36)	< 0.01
Tree count^{Na}	0.48 (0.05, 0.91)	0.03
Burned		
Intercept	0.11 (−0.30, 0.52)	
Nest tree height^{Nt}	0.71 (0.26, 1.16)	< 0.01

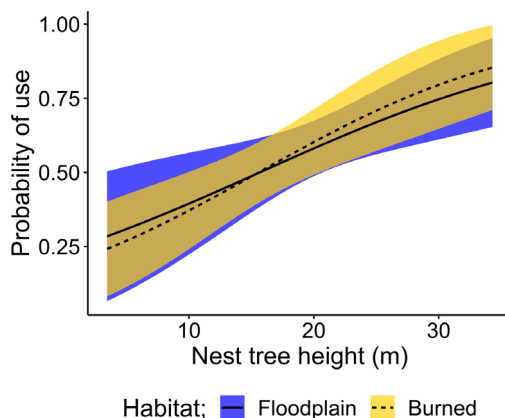|	Effect (CI)	*P* value
(B) Nest success		
Floodplain		
Intercept	4.99 (4.56, 5.42)	
Hatch day^{T}	−0.41 (−0.80, −0.02)	0.04
Canopy cover^{Na}	0.34 (0.03, 0.71)	0.07
Burned		
Intercept	5.90 (5.19, 6.61)	
Hatch day^{T}	−0.85 (−1.30, −0.40)	<0.01

Fig. 3. Predicted probability of Lewis's Woodpecker nesting in available nest trees depending on nest-tree height in the floodplain and burned forests. The shaded regions represent 95% confidence intervals.

$(\beta = -0.09, \quad SE = 0.01, \quad P < 0.001)$. We found higher attrition (i.e., loss of young) in floodplain (65%) than burned forest (50%) $(t = -2.2, P = 0.030)$.

Nest failures. We documented 42 nest failures out of 217 confirmed nest fates, including 29 in floodplain and 13 in burned forest. In both forest types, predation accounted for most (67%) nest failures. Combining definite (28 nests) with suspected (10 nests) predation events, almost all nest failures were due to predation (91%). We were not able to identify predator species. The remaining four nests in floodplain forest failed either due to a tree or branch falling ($N = 2$) or severe weather ($N = 2$; e.g., heavy rain and drought).

DISCUSSION

Adaptive habitat selection theory predicts greater or equal population density in habitat that provides higher fitness (Fretwell 1972, Martin 1998). However, the results of many studies have revealed mismatched habitat selection, with population densities higher in habitats with lower reproductive success (Chalfoun and Schmidt 2012). We found evidence of mismatched habitat selection, with densities of Lewis's Woodpeckers three times higher in floodplain than in the burned forest, but lower nest success in a floodplain forest. Saab and Vierling (2001) also found lower nest success for Lewis's Woodpeckers in cottonwood floodplain than burned sites (high intensity, 2–5 years post-fire), although nest success in the floodplain (46%) was lower than in our study (73%). Saab and Vierling (2001) suggested that low nest success in their floodplain forest study site may have been linked to the high agricultural use at and around nest sites and was caused by high predation rates. Recent work in British Columbia revealed nest success of Lewis's Woodpeckers in cottonwood floodplain forests more comparable to those in our study (79%;), but with low nest success in the burned forest (15%; high intensity and 10–15 years post-fire; Macfarland et al. 2019). Such low nesting success contrasts with those
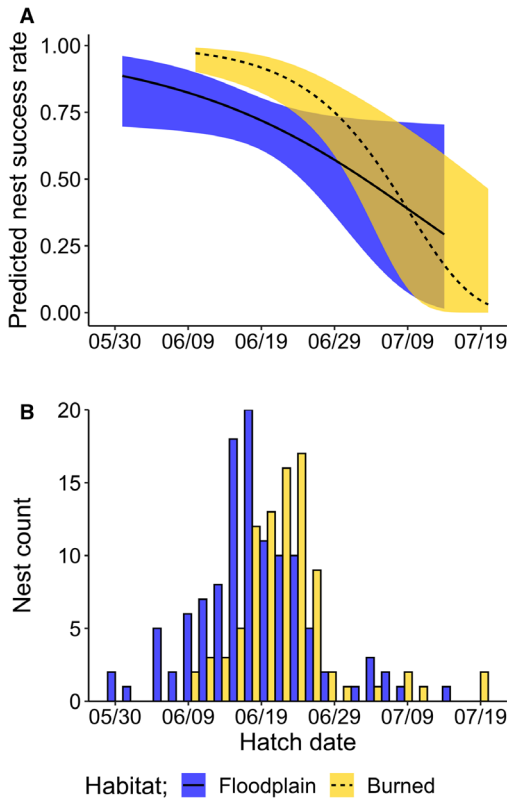
Fig. 4. Predicted nest success rate of Lewis's Woodpeckers by hatch date (A), and a number of nests at hatch date (i.e., when eggs hatch; B), across the nesting season in each habitat type. The shaded regions in (A) represent 95% confidence intervals.

of studies of nest success of other woodpecker species, with nest success often reported to be above 90% and rarely below 70% (Li and Martin 1991, Martin 1995, Stillman et al. 2019). The low nest success in burned forests reported by Macfarland et al. (2019) contrasts with other assessments regarding the importance of burned forests for Lewis's Woodpeckers. As such, additional comparisons of nest success in burned forests of differing ages and landscape conditions are needed to better understand any mismatch between the habitat preferences and breeding productivity of Lewis's Woodpeckers.

Lewis's Woodpeckers are widely considered burned-forest specialists (Bock 1970, Vierling et al. 2020), and several studies have focused on the impacts of fire age and salvage-logging activities on their nest success and densities across burned forests 1–12 years old post-fire and with mixed fire intensities (Saab et al. 2007, 2009). Saab et al. (2007) found that Lewis's Woodpeckers had significantly higher nest densities in logged forests, and Saab et al. (2009) found that nest densities were higher in partially logged patches 1–4 years post-fire than those 10–12 years post-fire. However, preferences switched to unlogged patches with older burned forests, likely due to falling snags in later years of the study that limited cavity availability for nesting. Saab et al. (2009) underlined the preference of Lewis's Woodpeckers for open overstories in partially logged forests where shrub densities were higher and potentially greater availability of arthropod prey. Additionally, Lewis's Woodpeckers nest success was lower in the burned forests that were 5–12 years post-fire than 1–4 years post-fire (Saab et al. 2007). Thus, the relative value of burned forests for Lewis's Woodpeckers varies by time since fire and with salvage-logging practices. In our study, we used greater variation in burned forests (i.e., fire intensity and time since fire) for assessing population densities. We caution, however, that despite the high densities of adult Lewis's Woodpeckers throughout our study system, the high nest success we found was limited to burned forests of a single, relatively old burn, and for a fire of high intensity. Similarly, our population estimates were also derived from a limited window of burned forest ages. Comparison of floodplain and burned forests requires a careful analysis of competing factors that include location, forest structure and composition, agricultural, and human use (e.g., farming, grazing, and logging) but also the nature and consequences of wildfires on the landscape. Drawing broad conclusions about the value of floodplain forests relative to burned forests for Lewis's Woodpecker nest success and population densities is difficult without considering human and wildfire impacts on the landscape along with fire age. Nevertheless, in our study system, the higher density, but lower nest success, of Lewis's Woodpeckers in floodplain compared to burned forests raises the question of whether lower nest success in the habitat with a higher density (i.e., floodplain forest) has contributed to their declining population.

We do not have definitive numbers for the other demographic rates affecting population trends of Lewis's Woodpeckers, but can use our observed fledging rates and hypothesized fledgling and adult survival estimates to predict population growth rates for our region. In our study area, Lewis's Woodpeckers produced an average of 2.19 ± 1.67 fledglings ($N = 67$) per successful nest. Fledgling and adult survival has not been estimated for Lewis's Woodpeckers, but adult survival has been estimated for congeneric Red-bellied (*Melanerpes carolinus*; 0.62) and Red-headed (*Melanerpes erythrocephalus*; 0.68) woodpeckers (Ingold 1989, Karr et al. 1990). In addition, Red-bellied Woodpeckers were found to have 92% of fledglings survive for the first 3 weeks post-fledging (Cox and Kesler 2012). Assuming a survival rate of adult Lewis's Woodpeckers similar to those of its congeners (0.65), a juvenile survival rate two-thirds that of adults (0.43; conservative estimate based on Cox and Kesler 2012), a nest success rate of 73%, and 2.19 fledglings per successful nest in our floodplain forest, the population of Lewis's Woodpeckers in our study would be stable ($\lambda = 1.00$; Pulliam 1988). However, applying similar calculations to the 46% nest success found by Saab and Vierling (2001) in their floodplain study in Colorado, the result would be a declining population ($\lambda = 0.82$; Pulliam 1988). Further, despite similar clutch sizes across forest types in our study area, higher attrition levels in the floodplain resulted in fewer fledglings per nest than in the burned forest. Although nest success and productivity were lower in floodplain forest, more fledglings/km^2 were produced in floodplain forest because of the greater density of nesting Lewis's Woodpeckers in floodplain than burned forest (15 vs. 5 fledglings, respectively, based on our density estimates and a 50/50 sex ratio). Our results, therefore, suggest that floodplain forests do not represent an ecological trap in our study area and likely serve as a buffer rather than contributing to population declines. However, similar nest success in our floodplain forest and in British Columbia (Macfarland et al. 2019), along with the lower nest success reported by Saab and Vieling (2001), suggests the possible importance of landscape context or internal degradation (e.g., grazing) impacts when evaluating the potential value of floodplain forests

for Lewis's Woodpeckers (Tewksbury et al. 2006).

In our study system, none of the cavity, nest-tree, or surrounding nest-area characteristics of Lewis's Woodpeckers explained variation in nest survival. The best predictor of nest success was hatch date. Factors that we did not consider may have contributed to lower nest success later in the breeding season, for example, changes in food availability, competition for nests, and predation rates during the breeding season could drive variation in nest survival over time. The results of other studies also suggest that nest initiation date influences nest success of Lewis's Woodpeckers in aspen woodlands (Newlon and Saab 2011), and in recently burned and old-growth cottonwood riparian (Zhu et al. 2012). Timing may be a crucial determinant in the competitive advantages of Lewis's Woodpeckers over other cavity-nesting species, such as with Red-headed Woodpeckers (*M. erythrocephalus*; Vierling et al. 2009) and European Starlings (*Sturnus vulgaris*) (Vierling 1998). Additionally, the timing of nest initiation also appears to be one of the few factors influencing nest success in other species of woodpeckers (Ingold 1994, Stillman et al. 2019, Fullerton et al. 2021). Although the results of some studies, like ours, have revealed no relationship between nest-site selection and nest survival, other studies of woodpeckers, even in burned habitat, have found nest-site characteristics associated with nest success (e.g., Li and Martin 1991, Hooge et al. 1999, Rolstad et al. 2000). Thus, the role of nest-site characteristics on woodpecker nest success remains worthy of additional study.

Several environmental factors may have contributed to differences in nest success and population densities in our two forest types. Nest competition with other secondary cavity nesters may prevent Lewis's Woodpeckers from selecting optimal cavities in floodplain forests (Vierling 1998, Macfarland et al. 2019). For instance, invasive European Starlings are ubiquitous throughout floodplain forests, but rarely found in burned habitats in our study area. European Starlings are aggressive cavity-nest competitors for Lewis's Woodpeckers (Vierling 1998) and other species of woodpeckers (Ingold 1994). European Starlings initiate nesting several weeks before

Lewis's Woodpeckers arrive in breeding areas (Ingold 1994), and we observed them inspecting cavities and harassing Lewis's Woodpeckers at our floodplain sites. The landscape surrounding the floodplain, or perturbations in the floodplain such as grazing, can influence the presence of European Starlings or other sources of nest failure. Floodplain forests away from human impacts may be particularly important nesting areas for Lewis's Woodpeckers, even if they are scarce on the landscape. Studies of the demography of Lewis's Woodpeckers in pristine floodplain forests are needed because nest success in such forests might be higher and reflect that preference for this forest type is adaptive over evolutionary time.

Predation was the leading cause of nest failure (91% of failed nests) in both floodplain and burned forest in our study as in previous studies (Vierling et al. 2020). We also observed fewer nests failing during incubation ($N = 14$) than during the nestling stage ($N = 26$) as in prior studies (Saab and Vierling 2001, Zhu et al. 2012). Early nest failure may provide opportunities for Lewis's Woodpeckers to re-nest, but we found few re-nesting attempts ($N = 9$). Other investigators have also reported either no or even fewer cases of re-nesting by Lewis's Woodpeckers after nest failure (Saab and Vierling 2001, Newlon and Saab 2011, Zhu et al. 2012). We did not monitor predation on adults, but did observe a Peregrine Falcon (*Falco peregrinus*) capture an adult Lewis's Woodpecker in mid-air while it was feeding above a nest tree. More detailed information about factors influencing the survival rates of adult and fledgling Lewis's Woodpeckers will improve our ability to predict areas of population growth and decline.

Management recommendations. Although nest success and population densities in our system reflected ecological mismatch, nesting productivity was sufficient to maintain Lewis's Woodpecker populations. Lower nest success in floodplain forests elsewhere suggests that managers need to better understand the factors that result in lower nest success in some floodplain forests, including competition, predation, food availability, variable cavity conditions, or some unidentified factors. In our system, both floodplain and burned forests provide important habitats for breeding Lewis's Woodpeckers. They experienced high nest success in both forest types, and at rates that we suspect contribute to the dispersal of fledging Lewis's Woodpeckers to other populations. Conserving and/or promoting both forest types could help counterbalance population declines elsewhere. Our results suggest that Lewis's Woodpeckers select nest sites in snags above 18 m in height in the floodplain and 20 m in the burned forest (using 0.50 snag use probability minimum cutoff). Snag retention in both forest types may be a determining factor in providing adequate nesting locations to Lewis's Woodpeckers.

Conservation of floodplain forests across western Montana is a complex issue because most are privately owned and managed. The persistence of floodplain forests in the future is uncertain, given issues like human development, drought, and control of water systems that prevent regeneration. Working with private landowners, particularly in retaining cottonwood snags, encouraging cottonwood recruitment, and protecting the development of sprouts and young trees (e.g., deer or cattle fencing exclosures) will help ensure the future use of these forests by Lewis's Woodpeckers.

Burned forests provide important habitat for Lewis's Woodpecker, occurring at a greater extent and distribution than floodplain forests and representing a widely available, yet ever-changing habitat. Although social pressures may dictate our tolerance for allowing forests to burn, Lewis's Woodpeckers benefit from fires on the landscape, particularly high-severity fires. However, we do not know when Lewis's Woodpeckers began occupying these burned forests and how nest success compares in either younger or older burned forests. Yet, our results suggest burned forests are important breeding areas for these woodpeckers for a minimum of 20 years post-fire. Salvage logging such forests without retaining some large snags (i.e., > 50 cm dbh and > 18 m tall) would likely preclude the use of severely burned forests by Lewis's Woodpeckers in their breeding range.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Model selection for nest-site selection within the "nest tree" set of explanatory variables for burned and riparian forest types. For riparian forest, we show the top eight variable combinations out of 64 total combinations.

Table S2. Model selection for nest-site selection within the "nest area" set of explanatory variables for burned and floodplain forest types. For both burned and riparian forests, we show the top eight variable combinations (16 and 17 total combinations in burned and riparian, respectively).

Table S3. Model selection for nest success within the "cavity and nest tree" set of explanatory variables for burned and riparian forest types. For riparian forest, we show the top eight variable combinations out of 128 and eight total combinations for the floodplain and burned forest types, respectively.

Table S4. Model selection for nest success within the "nest area" set of explanatory variables for burned and floodplain forest types. For both burned and riparian forests, we show the top eight variable combinations out of 16 total combinations.

Table S5. Model selection for nest success within the "temporal" set of explanatory variables for burned and floodplain forest types. All variable combinations are shown.