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# Forest management, forest vegetation, and climate influence nesting ecology of a focal bird species in the western USA

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## ABSTRACT

Landscape-scale forest restoration aims to restore ecological structure and function and provide habitat for wildlife. However, forest management likely has varying impacts across wildlife life stages, with consequences for population persistence. Using 10 years of nest (n = 294) survey data for a focal bird species, white-headed woodpecker (*Dryobates albolarvatus*), we assessed how forest management (tree removal and prescribed burning) at two spatial scales (stand [2.25 ha] and landscape [314 ha]), forest vegetation variables at three spatial scales (nest tree, local [0.4 ha], and landscape [314 ha]), and climate influenced nest initiation date, egg production, egg survival, and nestling survival. We applied Bayesian hierarchical mixed effects models to these data to identify and compare drivers at each life stage. None of the variables we considered influenced egg production; white-headed woodpeckers laid an average of four eggs. As the extent of the landscape with tree removal increased, nests initiated later. Egg survival was higher in nests with prescribed burning at the stand scale. Nestling survival was higher in sites that had been managed with burning and tree removal at the stand scale, but the relationship with burning switched to negative at the landscape scale. Only nestling survival was shaped by attributes of the nest cavity itself. Egg survival increased with increased variation in forest patch sizes at the landscape scale. Woodpeckers initiated nests earlier under warmer conditions, with previous August and September temperatures being particularly influential. Both egg and nestling survival increased with cumulative precipitation. While increased temperatures decreased egg survival, nestling survival peaked at an optimal maximum temperature (~32 °C). This study illustrates how forest management, forest vegetation, and climate factors affecting nesting ecology vary throughout the nesting season. Additionally, effects that switch directions (positive versus negative) across spatial scales indicate spatially dependent ecological processes (e.g., nest suitability versus adult foraging). This study provides a model for assessing the effects of forest management on bird population persistence by considering the nesting season as stages with distinct ecological limitations linked to spatially-dependent factors.

## 1. Introduction

For the past several decades, landscape-scale conservation and vegetation restoration efforts have become a widespread practice to restore ecosystem function, protect biodiversity, and increase ecosystem resilience to future change (Menz et al., 2013, Jones et al., 2021). While the emphasis of these programs is often on restoring vegetation structure and function, they also aim to support wildlife populations and communities (Schultz et al., 2012). As landscape-scale conservation and vegetation restoration builds momentum, there are a growing number of studies highlighting the benefits for wildlife communities (Latif et al., 2020b, Pavlacky et al., 2022).

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In the United States, especially in the western half of the country, landscape-scale restoration has focused on forested ecosystems (Ciuzio et al., 2013, Cyphers and Schultz, 2019, Phalan et al., 2019). A multitude of forces have disrupted forest dynamics in the United States since Euro-American colonization, including clear cutting, selective logging of large trees, grazing, and fire exclusion (Allen et al., 2002, Jones et al., 2018). These disruptions not only alter forested ecosystems but also put them at greater risk of large, high severity wildfire (Prichard et al., 2021, Ott et al., 2023). As a consequence, a variety of approaches are necessary to restore ecological functions, including thinning of trees, especially smaller trees, and re-introduction of understory fire (Hessburg et al., 2021, Prichard et al., 2021, Hagmann et al., 2021). Common management activities and resulting ecosystem states influence wildlife populations and communities and their ability to persist on the landscape (Shew et al., 2019, Pavlacky et al., 2022). Some management actions have the potential to reduce wildlife habitat in the short term while allowing for the maintenance or recovery of habitat in the long term by reducing the potential of large-scale high severity wildfire (Tempel et al., 2015, Latif et al., 2021, Jones et al., 2021, Davis et al., 2023).

Because of different life histories and habitat needs, the response of wildlife to forest management and the resulting vegetation structure and composition varies by species (Phalan et al., 2019, Latif et al., 2022). This may be because of life histories that are sensitive to habitat alteration (Drapeau et al., 2016) or because of different needs depending on wildlife species (e.g., different canopy cover preferences; Latif et al., 2022). Just as forest management and resulting habitat alteration can influence species differently, these factors may also shape population persistence within a species depending on season or life stage (Öberg et al., 2015, Milligan and McNew, 2022). For example, fledgling and adult black-backed woodpeckers (*Picoides arcticus*) in California, USA use different vegetation patches within post-fire landscapes. Fledglings use forest patches with more live trees and lower burn severity likely to avoid predation while adults forage in moderate to severely burned forest with greater availability of beetle larvae, but where predation risk is higher (Stillman et al., 2019). While these within-species effects of vegetation structure, composition, and management are key to population persistence, we have fewer examples of how management differentially impacts a species throughout multiple seasons or life stages than we do single life stages (e.g., adult occupancy and abundance; Latif et al., 2020b).

Not only can life stage or season influence responses within a species, but the spatial scale at which management and forest vegetation factors influence a species may also change throughout life stages or seasons. For example, different groups of grassland birds respond at different spatial scales to grassland restoration during the nesting season (Shew et al., 2019), with some scales of vegetation features and management influencing some species over others. Throughout the nesting season for birds, and within different life stages of a species, different spatial scales may influence persistence based on the changing needs of a species. Early in the nesting season, for example, the ability of adult birds to incubate eggs while foraging nearby may be paramount. Whereas later in the nesting season, nestlings may be left unattended more often while adults forage, making nest site suitability an important factor shaping nestling survival. The spatial scales of these effects may relate to ecological factors that affect persistence at different spatial scales, including nest microclimate, predation risk, and resource availability in the surrounding area used for adult foraging (Conway and Martin, 2000, Pasinelli, 2001, Wiebe, 2001, Öberg et al., 2015). Thus, management activities or forest vegetation features that have one effect at local or stand scales (e.g., reducing nearby predator habitat) may flip their effects at larger spatial scales (e.g., if they reduce foraging resources for adults). Finally, the effects of management and changing habitat occur in the context of other environmental variables that shape populations, including climate and underlying vegetation configuration.

In this study, we evaluated how the nesting ecology of a focal bird species, the white-headed woodpecker (*Dryobates albolarvatus*), was influenced by forest management in the Inland Pacific Northwest, USA (Oregon and Idaho). Forest management for this project is part of the Collaborative Forest Landscape Restoration Program (CFLRP; fs.usda.gov), which aims to manage large (>100,000 ha) areas of forested lands through collaborative science-based partnerships (Schultz et al., 2012, Hessburg et al., 2021). Fire suppression throughout the 20th century has altered these forests, leading to denser forests with homogenous structures, higher densities of fire-intolerant tree species, and high surface and ladder fuel loads (Hessburg et al., 2005, 2021, Savage et al., 2013, Battaglia et al., 2018, van Mantgem et al. 2018, Prichard et al., 2021). The loss of historical habitat due to fire suppression has led to an increased risk of population declines in white-headed woodpeckers with consequences for other species (Wisdom et al., 2000, Rich et al., 2004, Saab et al., 2004, Kozma, 2009). Additionally, associated changes in forest dynamics have created vulnerable conditions lacking resilience to rapidly changing wildfire and climatic conditions (Hessburg et al., 2005, Stephens et al., 2020, Prichard et al., 2021).

White-headed woodpeckers were selected for monitoring as a “focal” species that can potentially represent responses of multiple species because they are habitat engineers that excavate cavities used by other species (“primary cavity excavator”) (Saab et al., 2004, Thomsen et al., 2010, Hayward et al., 2016). White-headed woodpeckers are regionally endemic to dry pine (*Pinus* spp.)-dominant conifer forests of the Inland Pacific Northwest, which extend from the California Sierra Nevada to the Washington North Cascades (Garrett et al., 1996). White-headed woodpeckers rely on landscapes characterized by a mosaic of open- and closed-canopy forest containing live, dead, dying, and damaged trees for nesting and foraging (Wightman et al., 2010, Hollenbeck et al., 2011, Latif et al. 2015), as well as mature, cone-producing conifers for winter forage (Raphael and White, 1984). The landscape characteristics ideal for white-headed woodpecker nesting and foraging were historically generated and maintained by frequent, low- to moderate-severity fires (Wightman et al., et al., 2010, Hollenbeck et al. 2011, Latif et al., 2015, Latif et al., 2020a).

For this project, we specifically focused on nest initiation date, egg production, egg survival, and nestling survival to understand how forest management activities and environmental conditions influence the nesting ecology of white-headed woodpeckers, and how effects of management, vegetation configuration, and climate might change throughout the nesting season and at different spatial scales. We used a 10-year (2012–2021) dataset consisting of nest survey data in both managed (harvested/thinned or prescribed burned) and unmanaged forest locations. Using Bayesian statistical methods, we implemented mixed effects models for nest initiation date, egg production, egg survival, and nestling survival. All models included forest management factors at multiple spatial scales (stand and landscape scales), as well as forest vegetation variables at multiple scales representing nest-, local-, and landscape-scale features. Models for nest initiation date and egg production included pre-nesting climate variables using a stochastic antecedent modeling (SAM) approach (Ogle et al., 2015); egg and nestling survival models only included concurrent climate variables. We applied these models to white-headed woodpecker nest monitoring data to address two key questions: 1) What factors and spatial and temporal scales related to forest management and environmental factors influence white-headed woodpecker nest initiation date, egg production, egg survival, and nestling survival? And, 2) how do environmental drivers of population responses change throughout the nesting season? This study illustrates the importance of examining intra-specific effects of management and habitat needs throughout the nesting season, and it provides a framework for synthesizing information from long-term monitoring of avian nesting ecology to inform management that supports bird population persistence.

## 2. Materials and methods

### 2.1. Study site and species

We monitored white-headed woodpecker nesting ecology on three Collaborative Forest Landscape Program (CFLRP) projects. The three forest CFLRPs include the Southern Blues Restoration Coalition (44.0° N, 118.7° W, Malheur National Forest, Oregon), the Lakeview Stewardship Project (42.2° N, 120.2° W, Fremont-Winema National Forest, Oregon), and the Weiser-Little Salmon Headwaters Project (44.8° N, 116.5° W, Payette National Forest, Idaho; https://www.fs.usda.gov/restoration/CFLRP/index.shtml). The CFLRPs were established in 2012 with the aim of restoring open forest conditions in ecosystems dominated by ponderosa pine (*Pinus ponderosa*) (Kooistra et al., 2022). Each CFLRP has average targets of 205,000–420,000 ha of forest management activities, including pre-commercial thinning of small-diameter trees followed by prescribed burning within one to two years of thinning, and commercial harvest of large-diameter trees when stand densities needed to be further reduced. Burning has two forms: one type burns piles of wood and woody debris ("slash piles") following harvesting and thinning while the other ("broadcast burning") involves burning understory vegetation and fine fuels (including scattered logging debris) on the ground at low severity. The three forests are representative of the climatic conditions experienced by white-headed woodpeckers across their geographic range (Appendix S1, Figs. S1-S3).

### 2.2. Nest monitoring data

In each CFLRP, we established 27–30 transects approximately equally distributed in areas proposed for management and in areas with no active management during the study period (Fig. 1, Panel A). We assumed that management history was analogous between managed and unmanaged areas based on similarities in forest composition and structure. We selected transect point locations from a grid of points spaced 300 m apart, generated by a GIS that we overlaid across each CFLRP study area. Each transect extended 2700 m and consisted of 10 points spaced every 300 m along the transect. Transects did not necessarily form a straight line because point arrangement was dependent on management area configurations, vegetation type, and habitat suitability.

To locate white-headed woodpecker nests, field technicians used call-broadcast surveys consisting of white-headed woodpecker drumming and calling to elicit territorial responses from breeding adults (for details see: Mellen-McLean et al., 2015, Latif et al., 2015). We conducted call-broadcast surveys 2–3 times at each transect point from 6 May to 6 July 2012–2021 and searched for nests by meandering within a 200 m belt width centered on transects (Dudley and Saab, 2003), completing 1–2 searches per transect each year. We generally conducted broadcast surveys between 0530 and 1100 local time and nest searches between 0530 and 1330. Once we detected an adult white-headed woodpecker, we followed individuals up to 1 km from transects. We searched for and

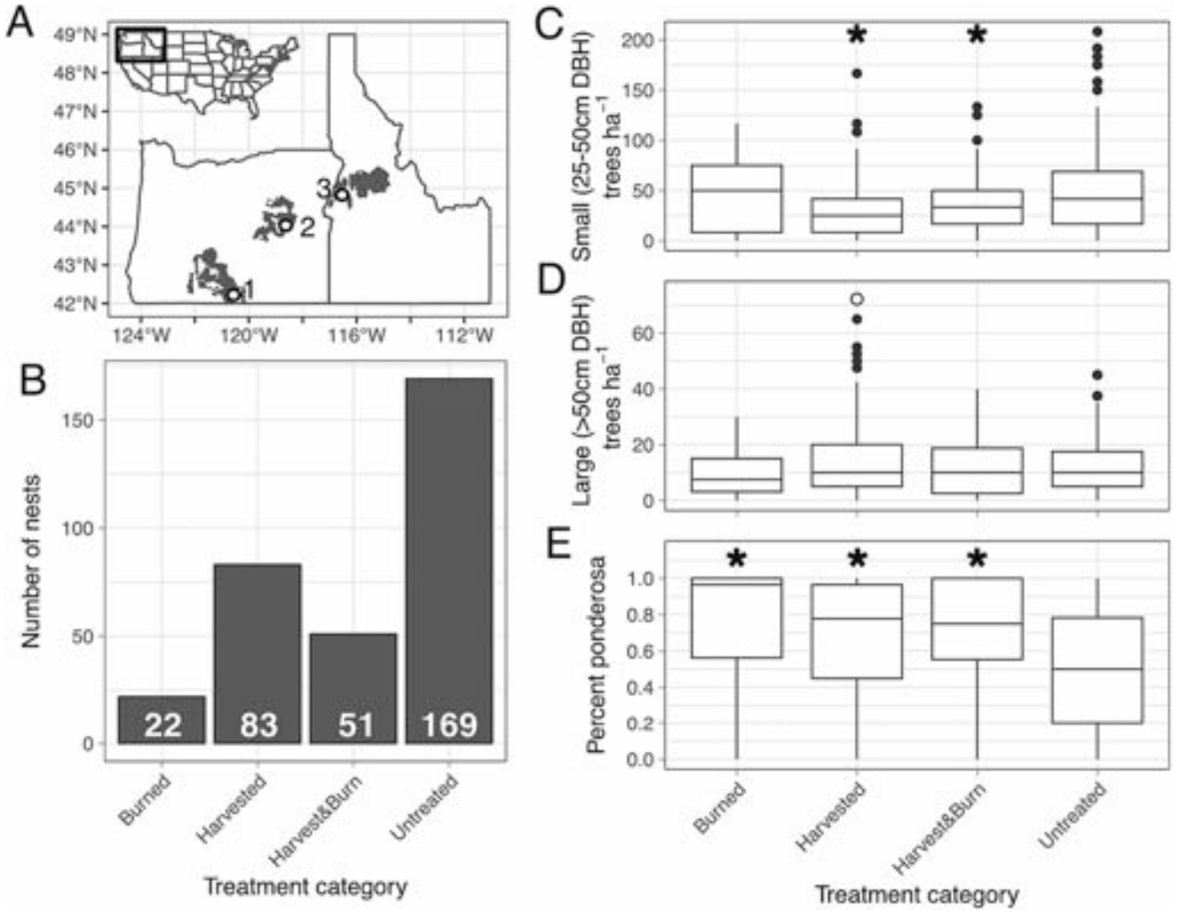

**Fig. 1.** A) The locations of the three Collaborative Forest Landscape Restoration Program (CFLRP) management areas in Oregon and Idaho (survey period 2012–2021): 1 = Fremont-Winema National Forest, 2 = Malheur National Forest, 3 = Payette National Forest. B) Across the three forests, white-headed woodpeckers were located such that most nests were in unmanaged areas, with the rest located in areas that were managed with prescribed burning, tree harvesting and thinning, or the combination of these two management actions. C) Locations with harvest and a combination of harvest and burn management types have fewer small trees; D) locations with harvest management have higher large tree density; and E) all areas that received management activity have higher percentage of ponderosa pine trees than unmanaged sites (asterisks in C-E indicate values that are different from unmanaged sites).

located nests in the vicinity of all transect points but focused especially in areas where white-headed woodpeckers had been detected, including previous years' nest locations. Once nests were located, we determined the stage of the nest (excavating/pre-laying, laying, incubating, nestling) based on adult behavior or by viewing nest contents. We then revisited nests 1–2 times weekly for approximately 30 min per visit to record nest status and determine nest fate as successful or failed.

To determine nest contents (eggs, nestlings), we viewed nests using a wireless video camera system attached to a telescoping pole (Luneau and Noel, 2010). We determined nest initiation date, when possible, directly from nest-visit observations and video camera evidence, and indirectly by back-calculating from egg-nestling or nestling-fledgling transitions using published nest stage data for white-headed woodpeckers (Garrett et al., 1996). We determined fledgling numbers directly at each nest by counting fledglings attended by adults. When we visited empty nests with no evidence of predation later in the breeding season, we estimated fledgling numbers based on the number of observed well-developed nestlings observed during previous visits. (e.g., Kozma et al., 2017, Stillman et al., 2019). We viewed 82% of nest cavities with a video camera to confirm final nest contents.

### 2.3. Explanatory variables

We compiled data on multiple variables that could explain the observed variability in nest initiation date, egg production, egg survival, and nestling survival. The variables include forest management factors at two spatial scales (the stand [2.25 ha] and the landscape [314 ha]), forest vegetation variables observed at three spatial scales (nest tree, local [0.4 ha] and landscape [314 ha]), and potential climate drivers. Fig. 2 visually depicts the spatial and temporal scales of forest management, vegetation, and climate covariates for each model and their ecological significance. We summarize key variables that were incorporated into our final models, described below.

#### 2.3.1. Nest attribute variables

To evaluate the effects of nest attributes on nesting ecology, we collected information during nest surveys about the nest cavity and timing. Nest information included height above the ground (in meters) of the cavity entrance, cavity orientation (true bearing in degrees), nest tree species, and nest initiation date (the date the first egg was laid).

#### 2.3.2. Local-scale forest vegetation variables

To determine which local-scale forest vegetation variables influenced nesting ecology, we collected information during nest surveys on tree composition and density within 50 m (0.4 ha) of the nest (Mellen-McLean et al., 2015). Tree variables included the density of all trees in two size classes (25–50 cm DBH and > 50 cm DBH; DBH = diameter-at-breast height [~1.4 m]) and the percent of ponderosa pine. Vegetation surveys typically occurred once before and once after management activity. When forest management occurred before vegetation surveys, we used the resulting stumps and derived relationships between stump diameter and tree DBH to infer pre-management tree density by size class. Distributions of tree density and percent ponderosa pine in relation to management actions are visualized in Fig. 1, Panels C-E.

#### 2.3.3. Stand-scale management variables

At the stand scale (2.25 ha) around each nest, we determined the timing and status of restoration management activities (thinning/harvesting and burning) using a combination of field observations, remotely sensed imagery, and the US Forest Service Activities Tracking System (FACTS, https://www.fs.usda.gov/managing-land/natural-resource-manager) verified during concurrent field surveys (Fig. 1, Panels C-E) and supplemented with Google Earth Pro (Earth version 7.3.6) imagery where needed to confirm activities. FACTS is an application used for

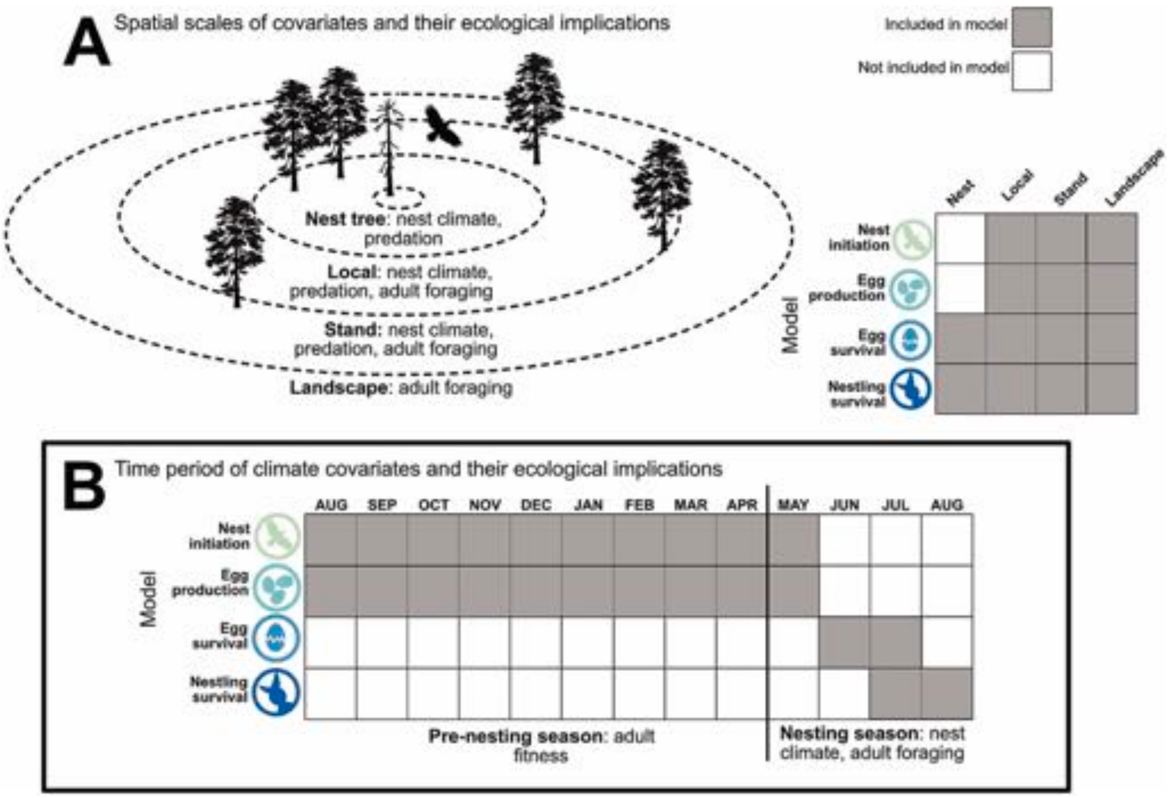

**Fig. 2.** A) The spatial scales of covariates in each of the four models for white-headed woodpecker nesting ecology (nest initiation date, egg production, egg survival, and nestling survival; grey boxes in grid) and B) the temporal scales for climate covariates in each of the four models, along with ecological implications of all variable groups.

documenting the history of fire, fuels, silviculture, and invasive species related to management activities. We compiled management activities since 2002 (i.e., including the 10 years prior to CFLRP activities) within a 5 × 5, 30-m pixel area (2.25 ha) surrounding each nest. We chose this scale because it likely represents a stand of trees with similar structure, composition, and management activities. We grouped multiple FACTS activity codes based on their ecological significance to white-headed woodpeckers and created a categorical variable to describe management activities. These categories included tree removal-related activities (harvesting and thinning, and one nest with pile burning only at the stand scale, since this activity follows tree removal activities) as "harvest" and all broadcast or understory burning as "burn" management. We also included a category representing the combination of these two management types: "harvest and burn" (Fig. 1, Panel B).

### 2.3.4. *Landscape-scale management variables*

To determine how responses to management vary across spatial scales, we generated landscape-scale management extent variables. We used ArcMap 10.7.1 (ESRI, 2019), FACTS data, and FRAGSTATS 4.2 (McGarigal et al., 2012) to characterize forest landscape management activity at a 1000 m radius (314 ha) surrounding each nest location. We chose this scale based on previous literature (Wightman et al., 2010, Hollenbeck et al., 2011, Latif et al., 2015) and radio-telemetry data from white-headed woodpeckers in the region (Wright et al., *unpublished data*). Within the nest landscape, we quantified the percentage of the area that received management actions in two categories: harvest or burn. The stand- and landscape-scale management variables, though derived from the same data sources (FACTS) represent two distinct ecological limitations: processes that likely influence the more immediate area around the nest (e.g., nest predation) and those at a broader scale that likely influence adult foraging.

### 2.3.5. *Landscape-level forest vegetation variables*

To determine the influence of landscape-scale variables (314 ha) on nesting ecology, we generated additional covariates for each model using LANDFIRE Existing Vegetation Canopy Cover attributes from LF 2012 to reflect pre-management (i.e., through 2012) forest conditions and LF 2019 to reflect post-management (i.e., 2013–2019) forest conditions (USDA and USGS, 2022). We used ArcMap 10.7.1 (ESRI, 2019) and FRAGSTATS 4.2 (McGarigal et al., 2012) to characterize forest landscape composition and configuration metrics at a 1000 m radius (314 ha) surrounding each nest location (Appendix S2, Table S1).

### 2.3.6. *Climate variables*

We generated monthly temperature and precipitation data for all transects with nests from 2011 to 2021 using ClimateNA (Wang et al., 2016). ClimateNA produces scale-free point data suitable for characterizing climate variables at local management unit scales. For the nest initiation date and egg production models, we obtained the prior season maximum temperature and total monthly precipitation for each of the previous 10 months (August-May). For the egg and nestling survival models, we also determined the monthly maximum temperature and total cumulative precipitation for each nest stage, taking the monthly average of temperature and the cumulative precipitation across months (1–2 months, on average) when a stage spanned more than one month.

### 2.3.7. *Final variables used in models*

Prior to combining variables into models, we verified that all variables were not highly correlated with each other based on Pearson correlation coefficients (highly correlated: $>$ 0.60, Appendix S2, Figs. S1-S3). In particular, because landscape metrics are often highly correlated with each other (Appendix S2, Figs. S4-S6, S7-S8; Cushman et al., 2008), we chose from a candidate list of metrics for each response variable (nest initiation date, egg production, egg survival, and nestling survival) based on preliminary frequentist variable selection using AICc (Akaike Information Criterion; Akaike, 1974, Heinze et al., 2018). To perform variable selection, we created a set of models with only one landscape metric covariate for each response. We then ranked the models by AICc (lower values being better models) and selected the top one to three landscape metrics ("models") based on their lack of correlation with other covariates and their lack of redundancy with landscape metrics that were not correlated with any other metrics (Appendix S2, Tables S2-S5). All covariates considered for all models and their inclusion and reasons for removal from each model can be found in Appendix S2, Fig. S9. Prior to modeling, we standardized all continuous-valued covariates based on their mean and standard deviation, and we used standardized covariates to aid in model fitting and model interpretation. We set the "baseline" level for all categorical covariates as the level with the greatest number of observations for similar reasons. We imputed missing covariate data (<1–9% of covariate data were missing, depending on the variable; see below for more details; (Ogle et al., 2013)).

### 2.3.8. *Stage-specific hierarchical statistical models*

To model nest initiation date, egg production, egg survival, and nestling survival, we created separate models for each of these four responses; all models included relevant covariates and covariate interactions. Not all models contained the same set of covariates; we selected covariates for each model because of their potential relevance to that life stage (Appendix S2, Fig. S9). We structured the models to accommodate the response variable properties and the sampling design and implemented all models in a hierarchical Bayesian framework. Bayesian methods allowed us to simultaneously impute missing covariate data (Ogle et al., 2013, Dorazio, 2016) and to incorporate the effects of antecedent climate on nest initiation date and egg production using a stochastic antecedent modeling (SAM) framework (Ogle et al. 2015). The hierarchical aspect allowed us to represent the spatial non-independence of monitoring data crossed with the year of sampling. For each response variable, we considered how forest management activities at two spatial scales (stand and landscape) influenced white-headed woodpecker nesting ecology. We also considered an ecologically appropriate set of nest attributes, along with local-, and landscape-scale forest vegetation covariates, climate (concurrent or antecedent), and ecologically meaningful variable interactions (Appendix S2, Fig. S9). The nest initiation date and egg production models included variables at scales that presumably influenced adult fitness, including landscape-scale management, antecedent climate (Ogle et al., 2015), and local- and landscape-scale forest vegetation variables. For egg and nestling survival, we considered variables at scales that presumably influenced adult foraging ability and nest site suitability (microclimate and predation risk), including stand- and landscape-scale management, nest attributes, and local- and landscape-scale forest vegetation variables, and the effects of temperature and precipitation that encompassed the temporal period specific to each nest (i.e., the months in which a particular nest contained eggs or nestlings) (Fig. 2).

### 2.3.9. *General form of linear predictor*

The models for all four response variables (nest initiation date, egg production, egg survival, and nestling survival) involve either a linear regression or a generalized linear modeling approach, all of which link the expected response to a linear predictor. For all models, the linear predictor, $\eta$, for observation $i$ has the general form:

$$\eta_i = \beta_0 + \sum_{j=1}^{N}\beta_j X_{j,i} + \sum_{j=1}^{N}\sum_{k=j+1}^{N}\beta_{jk}X_{j,i}X_{k,i} + \alpha_{T(i)} + \lambda_{S(i)} + \varepsilon_{t(i)} + \gamma_{y(i)} \tag{1}$$

where $j$ (or $k$) denotes the covariate index, and $X_{j,i}$ is the standardized value for covariate $j$ for $N$ different covariates. Parameters of interest include the overall intercept, $\beta_0$, the covariate main effects, $\beta_j$ terms, and the 2-way interactions among select covariates, $\beta_{jk}$ terms; not all 2-way interactions are included, which is analogous to setting associated $\beta_{jk}$ terms to zero. See Appendix S2, Fig. S9 for the list of continuous-valued covariates and 2-way interactions included in each model. The categorical fixed effects of forest management type and nest tree species are indicated by $\alpha$ and $\lambda$, respectively, with $T(i)$ and $S(i)$ indicating the forest management treatment factor level, $T$ (e.g., unmanaged, harvested, burned, or harvested and burned), and $S(i)$ indicating the nest tree species, $S$ (e.g., ponderosa pine, western juniper, true fir, Douglas-fir, or quaking aspen) associated with observation $i$. However, $\lambda$ is only included in the egg survival and nestling survival models. Random effects for transect and year are denoted by $\varepsilon$ and $\gamma$, respectively, where $t(i)$ and $y(i)$ indicate transect $t$ and year $y$ associated with observation $i$, respectively.

### 2.3.10. General approach to modeling fixed and random effects

For the effects of the categorical forest management types, $\alpha_T$, and nest tree species, $\lambda_S$, we treated the first level ($T = 1$ for unmanaged and $S = 1$ for ponderosa pine) as the reference cells such that $\alpha_1 = 0$ and $\lambda_1 = 0$. We assigned relatively non-informative, normal priors (mean of zero and large variance) to the effects for the other levels, i.e., for $\alpha_T$ for $T = 2$ and 3 and for $\lambda_S$ for $S = 2, 3, 4,$ and 5. We hierarchically centered the random effects of transect, $\varepsilon_t$, about the overall intercept, $\beta_0$, based on a normal distribution. We assigned the year random effects, $\gamma_y$, a normal distribution with mean zero and an unknown (to be estimated) variance; we applied sum-to-zero constraints to the year random effects to ensure identifiability of the overall intercept and random effects (Ogle and Barber, 2020).

We completed model specification by assigning relatively non-informative, normal priors to the overall intercept, $\beta_0$, all main effects, $\beta_j$ terms, and all interaction effects, $\beta_{jk}$ terms, in Eqn (1). We assigned wide (vague) uniform priors to all standard deviations (Gelman, 2006) introduced through the data model (likelihood) and hierarchical priors for the random effects.

Because missing covariate data were a small percentage for only a few covariates (1–2 covariates in each model; ~1–9% of a covariate was missing, depending on covariate and model) and because these missing data were assumed to be missing at random, we imputed missing covariate values in the model. To do so, we allowed missing covariate values to vary stochastically via a normal distribution with a scalar mean and variance for each covariate. The means were assigned relatively noninformative uniform priors spanning the observed values of each covariate and the standard deviations were assigned wide (vague) uniform priors.

### 2.3.11. Nest initiation date and egg production model

Our model for nest initiation date assumed that the log-transformed initiation date followed a normal distribution with a mean given by the general model described in Eqn (1). The model for egg production assumed a Poisson distribution for the observed count data (number of eggs reported in a nest). We modeled the mean of the Poisson distribution (e.g., $\mu$) as $\log(\mu) = \eta$, with $\eta$ given by Eqn (1); or $\mu = \exp(\eta)$.

Nest initiation date and egg production are influenced by adult fitness before the nesting period (Harrison et al., 2011), thus we included covariates relating to a nest's suitability for adults, including landscape-scale management, local- and landscape-scale forest vegetation covariates, and antecedent climate. For egg production, we also considered stand-scale management and nest initiation date as drivers of egg production (Appendix S2, Fig. S9; Rossmanith et al., 2007). Because we did not know which past months determined adult nesting fitness, and adults have seasonally variable food requirements (e.g., Herrera, 1982), we modeled antecedent climate effects using a SAM approach (Ogle et al., 2015). An antecedent climate variable (maximum temperature and precipitation) associated with a particular observation is computed as a weighted average of the corresponding monthly climate values during each previous month since the end of the last nesting period. Each month is assigned an importance weight that describes the importance of that month's climate variable for initiation date or egg production; these importance weights are constrained to add to one across all prior months. We only considered the months since the previous nesting period (previous 10 months, August-May) because nesting adults may have been fledglings from the previous year. Following initial model runs, if months farther in the past had low importance weights, we removed those months from subsequent model runs.

### 2.3.12. Egg and nestling survival models

To model egg survival, we assumed that the observed number of nestlings (total number of "successes") followed a binomial distribution with probability, $p$, of an egg surviving to the nestling stage, and the total number of "trials" given by the initial number of eggs in a nest. Similarly, to model nestling survival, we assumed a binomial distribution for the observed number of fledglings given probability, $f$, of a nestling surviving and total trials equal to the number of observed nestlings in a nest. We modeled the nest-level logit-probabilities, $\text{logit}(p)$ and $\text{logit}(f)$, according to the linear predictor, $\eta$, in Eqn (1), with covariates as summarized in Appendix S2, Fig. S9.

### 2.3.13. Model implementation, convergence, and goodness of fit

We implemented the models in JAGS (JAGS version 4.3.1, Plummer, 2003) and R (version 4.2.0, R Core Team, 2020) via the jagsUI (version 1.5.2; Kellner, 2021) package. We simulated three parallel Markov chain Monte Carlo (MCMC) sequences for all models. We ran initial models for a small number of iterations (~4000 per sequence) to evaluate initial MCMC behavior and to determine the number of samples required to sufficiently explore the posterior parameter space (Raftery and Lewis, 1995) using the raftery.diag() function (Raftery and Lewis, 1992) in the coda package (version 0.19.4; Plummer et al., 2006). We then adjusted the number of iterations and burn-in period for each model based on results of this diagnostic test. For the final model runs, we confirmed model convergence by visually inspecting history plots, posterior distributions, and autocorrelation plots of sampled model parameters. We quantitatively evaluated convergence of the MCMC sequences to the posterior distribution using the Gelman-Rubin statistic ($\widehat{R}$; Gelman and Rubin, 1992)); $\widehat{R} < 1.1$ was our criteria for convergence.

For model validation, we performed a graphical posterior predictive check (Conn et al., 2018), then determined a goodness-of-fit metric based on the correlation between observed and simulated predicted response values from each model (e.g., Gelman et al., 2020, Guo et al., 2020, Peltier et al., 2022). Finally, we did not include an effect for each of the three CFLRP locations in the model, but these larger regional locations may experience different nesting ecologies. Therefore, to quantify the amount of variation explained by CFLRP location (3 locations; two in Oregon, one in Idaho), we fit the residuals of each model to a categorical variable of CFLRP location (e.g., Patrick et al., 2009) and verified that each predicted response did not have consistently higher or lower values based on CFLRP location.

### 2.3.14. Determining variable importance

We evaluated posterior median and central 95% Bayesian credible intervals (BCIs) for each model; covariate effects were deemed important if their BCI excluded zero. We further verified variable importance by computing Bayesian $p$-values for each covariate with a cutoff for variables that were non-zero (positive or negative) in $\geq$95% of iterations. During the Bayesian model fitting, for both quadratic terms and covariate interactions, we verified that any non-zero effect had an ecologically realistic pattern (e.g., negative quadratic temperature or precipitation terms suggest an optimal value; whereas positive quadratic terms have little ecological relevance) and were not driven by values at the extremes of the covariate distributions where there were few observed values. We removed any terms from the model that did not make ecological sense or that were driven by extreme values (for interactions) and re-ran all modeling steps (setting initial values, checking for convergence, and evaluating goodness-of-fit as described above, Appendix S2, Fig. S9).

### 2.3.15. Data and analysis reproducibility

We prepared data using packages tidyverse (version 1.3.0, Wickham et al. 2019), here (version 1.0.1, Muller, 2020), lubridate (version 1.8.0; Grolemund and Wickham, 2011), readxl (version 1.4.0; Wickham and Bryan, 2022), and reshape2 (1.4.4; Wickham, 2007). We assessed model outputs using coda and mcmcplots (version 0.4.3, McKay Curtis, 2018). We created visuals using the patchwork package (version 1.1.1; Lin Pedersen, 2020). We performed all pre-modeling variable selection and correlation analyses with GGally (version 2.1.1; Schloerke et al., 2021), glmmTMB (version 1.1.2; Brooks et al., 2017), MuMIn (version 1.43.17; Barton, 2020), DHARMa (version 0.3.3.0; Hartig, 2020), emmeans (version 1.8.2; Lenth, 2022), glmm (1.4.4; Knudson, 2022), caret (version 6.0.93; Kuhn, 2022), and effects (version 4.2.0; Fox and Hong, 2009). We ran all models on Northern Arizona University's high-performance computing cluster, "Monsoon". All raw data and code used to generate the data cleaning and analysis process can be found in reproducible format in Miller-ter Kuile et al. (2023).

## 3. Results

### 3.1. Data summary

We located 363 white-headed woodpecker nests from 2012 to 2021. We visited nests 6 times each on average (range: 1–20 visits per nest) totaling 2230 visits. Visits lasted 26 min on average (range: 1–375 min per visit) and nests were viewed with a camera during 65% of visits. Overall, 73% (±3% SE yearly survival average) of nests survived to the fledgling stage. Nests that survived to each stage (egg production, nestlings, fledglings) typically had 3.9 ± 0.1 eggs, 2.4 ± 0.1 nestlings, and 2.1 ± 0.1 fledglings (Fig. 3). Most nests that did not produce fledglings ("failed nests") did so with an unknown cause (70%; 61 out of 87 nests that failed). Known causes of failure were predation (including by black bears (*Ursus americanus*), common ravens (*Corvus corax*), and chipmunks and squirrels, *Sciuridae* spp.) (14%; 12 of 87 failed nests). The remaining 14 nest failures (16%) were attributed to weather-related events or adult abandonment. Due to imperfect observation of nest initiation date and nest contents throughout stages, we had different sample sizes of nests for each model: 294 for nest initiation date, 140 for egg production and egg survival, and 271 for nestling survival.

### 3.2. MCMC behavior

MCMC sequences for parameters in all models converged ($\widehat{R}$ for all parameters $< 1.1$; Appendix S3, Figs. S1-S4). Based on Raftery diagnostics, we adjusted model iterations and burn-in so that all models had enough iterations to accurately estimate parameter medians and 95% BCIs. We report posterior medians and 95% BCIs for covariate effect estimates ($\beta$ terms) in results and figures.

### 3.3. Nest initiation date and egg production models

The nest initiation date model explained 33% of the variance in nest initiation date (Appendix S3, Fig. S5, Panel B). The large amount (66%) of unexplained variance suggests nest initiation is a highly stochastic process or that important variables contributing to nest initiation were not measured and included in models. Median nest initiation date was Julian date 157 (95% BCI = [145, 175]; June 6–7, depending on the year). Based on the posterior predictive check, the model predicted slightly later median nest initiation dates than the observed data (Appendix S3, Fig. S5, Panel A). Results for all model covariates can be found in Table 1. White-headed woodpeckers initiated nests later as the percent of harvested landscape (314 ha) increased ($\widehat{\beta}_{\text{PercHa}} = 0.01$; 95% BCI = [0.00, 0.02], Fig. 4, Panel A) and initiated earlier under warmer antecedent (past) maximum temperatures ($\widehat{\beta}_{\text{TmaxAnt}} = -0.15$; 95% BCI = [-0.42, −0.04], Fig. 4, Panel B). Temperatures during May of the current nesting period as well as the previous nine months contributed relatively equally to the temperature effect, though the previous August and September had relatively stronger effects than other months (mean of 12 and 14% of total effect, respectively, compared to 4–9% for all other months), such that a warm previous August and September (late summer and early fall) influenced woodpeckers to initiate nests earlier (Fig. 4, Panel C). A slightly smaller amount of variation was attributed to the random effects of transect ($\widehat{\sigma}^2_{\text{transect}} = 0.01$; 95% BCI = [0.00, 0.02]) than year ($\widehat{\sigma}^2_{\text{year}} = 0.02$; 95% BCI = [0.01, 0.05]). CFLRP location did not explain a significant amount of residual variance (0.5% residual variance; Appendix S3, Fig. S9).

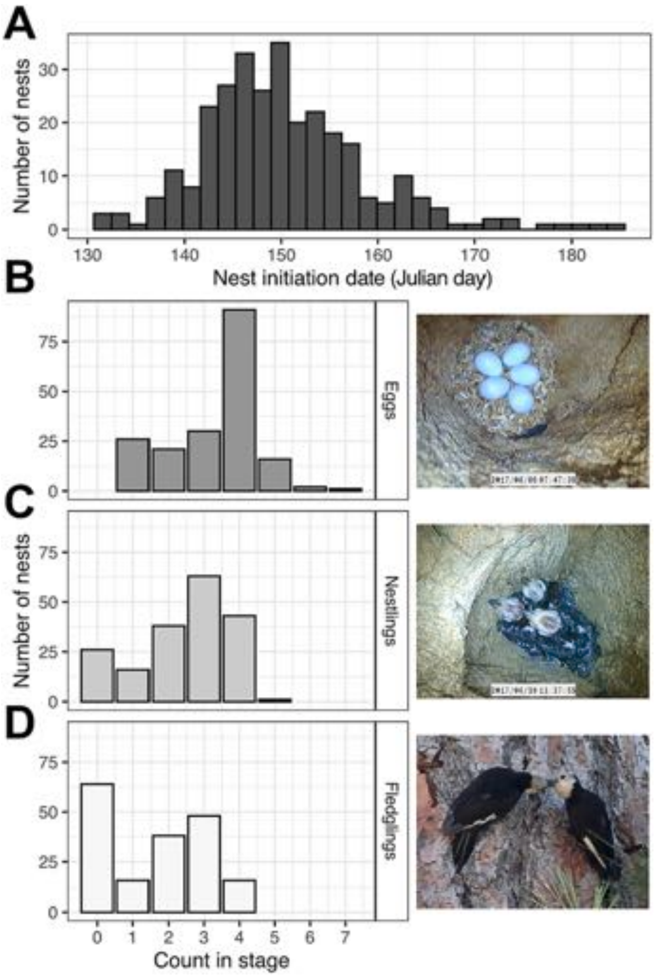

**Fig. 3.** For white-headed woodpeckers across the three CFLRP management areas (see Fig. 1), data are summarized across all nests to show the empirical distributions of: A) nest initiation date (Julian date), B) number of eggs, C) number of nestlings, and D) number of fledglings in individual nests. Photo credit: J. Dudley and A. Kehoe.

The egg production model explained 21% of the variance in egg production (Appendix S3, Fig. S6, Panel B). Based on the posterior predictive check, the model predicted a lower mean number of eggs per nest than observed (Appendix S3, Fig. S6, Panel A). The estimated median number of eggs per nest was 3.40 (95% BCI = [2.16, 5.49]). No forest management covariates influenced egg production, nor did any forest vegetation or climate variables (Table 2). A similar amount of variation was attributed to transect ($\widehat{\sigma}^2_{\text{transect}} = 0.04$; 95% BCI = [0.00, 0.13]) and year ($\widehat{\sigma}^2_{\text{year}} = 0.04$; 95% BCI = [0.00, 0.16]). CFLRP location did not explain a significant amount of residual variance (0.2% residual variance, Appendix S3, Fig. S10).

**Table 1**
Nest initiation date model results, showing covariates included in the model, and the posterior estimates (median, 95% Bayesian credible interval [BCI] limits, and Bayesian p-value) for each covariate main effect or interaction effect.

| *Covariate category* | *Covariate* | *Median* | *Lower BCI* | *Upper BCI* | *Bayesian p-value* |
|---|---|---|---|---|---|
| Landscape-scale management | **Percent of landscape harvested** | **0.01** | **0.00** | **0.02** | **0.04** * |
| | Percent of landscape burned | 0.00 | −0.01 | 0.01 | 0.42 |
| Local-scale forest vegetation | Large tree density | 0.00 | −0.02 | 0.02 | 0.36 |
| | Small tree density | 0.00 | −0.04 | 0.02 | 0.49 |
| | Percent ponderosa forest | 0.00 | −0.01 | 0.01 | 0.41 |
| Landscape-scale forest vegetation | Forest patch size CV | 0.00 | −0.01 | 0.01 | 0.31 |
| | Contagion index | 0.00 | −0.01 | 0.01 | 0.25 |
| | Largest patch index | 0.00 | −0.01 | 0.01 | 0.24 |
| | Number of patches | 0.00 | −0.01 | 0.00 | 0.13 |
| | Mean forest patch size | 0.00 | −0.01 | 0.01 | 0.44 |
| Climate | **Maximum temperature** | **−0.15** | **−0.42** | **−0.04** | **0.01** ** |
| | Precipitation | 0.04 | −0.05 | 0.26 | 0.19 |
| Interactions | Large tree density × perc. ponderosa | 0.00 | −0.01 | 0.01 | 0.29 |
| | Small tree density × perc. ponderosa | 0.00 | 0.00 | 0.01 | 0.16 |
| | Small tree density × maximum temperature | 0.04 | −0.03 | 0.11 | 0.12 |
| | Large tree density × maximum temperature | 0.00 | −0.05 | 0.06 | 0.49 |
| | Percent of landscape harvested × percent burned | 0.00 | −0.01 | 0.00 | 0.21 |
| | Temperature × precipitation | −0.18 | −0.60 | 0.07 | 0.08 |

*Bolded values indicate significant effects (Bayesian p-value < 0.05).

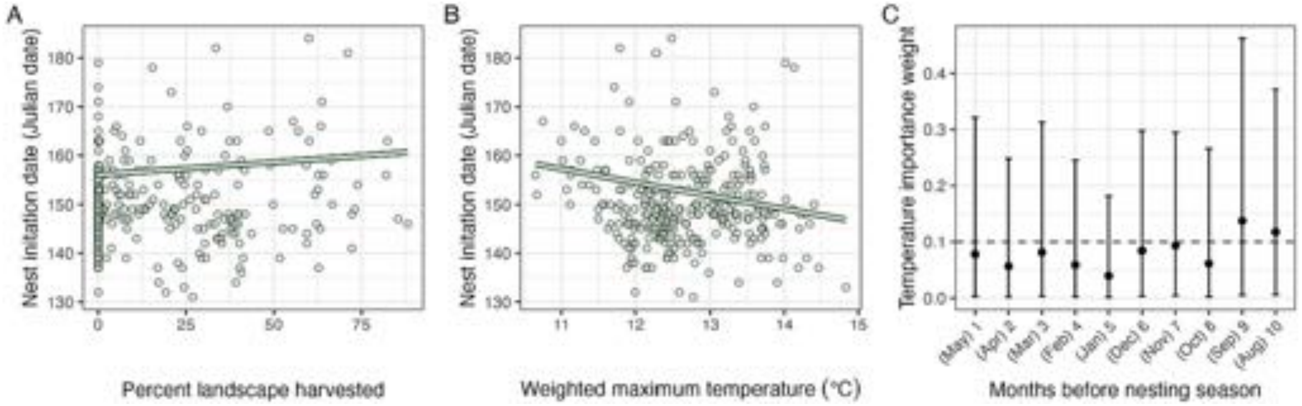

**Fig. 4.** Marginal effects of the most important variables shaping nest initiation date for white-headed woodpeckers in the three CFLRP locations. These variables include A) percent of landscape managed with harvesting B), and maximum temperature. C) The temperature effect was shaped by warmer temperatures in the previous year's August and September.

**Table 2**
Egg production model results, showing covariates included in the model, and the posterior estimates (median, 95% Bayesian credible interval [BCI] limits, and Bayesian p-value) for each covariate main effect or interaction effect.

| *Covariate category* | *Covariate* | *Median* | *Lower BCI* | *Upper BCI* | *Bayesian p-value* |
|---|---|---|---|---|---|
| Stand-scale management | Treatment type: Burn | 0.07 | −0.42 | 0.53 | 0.38 |
| | Treatment type: Harvest | 0.21 | −0.13 | 0.56 | 0.11 |
| | Treatment type: Harvest&Burn | 0.03 | −0.53 | 0.57 | 0.46 |
| Landscape-scale management | Percent of landscape harvested | −0.06 | −0.22 | 0.10 | 0.22 |
| | Percent of landscape burned | 0.01 | −0.18 | 0.20 | 0.46 |
| Nest attributes | Nest initiation day | −0.04 | −0.14 | 0.05 | 0.19 |
| Local-scale forest vegetation | Large tree density | 0.01 | −0.29 | 0.34 | 0.45 |
| | Small tree density | 0.04 | −0.26 | 0.41 | 0.36 |
| | Percent ponderosa forest | −0.03 | −0.13 | 0.08 | 0.31 |
| Landscape-scale forest vegetation | Forest patch size coeff. variation | 0.03 | −0.08 | 0.15 | 0.27 |
| | Contagion index | −0.01 | −0.15 | 0.12 | 0.43 |
| | Largest patch index | −0.02 | −0.13 | 0.10 | 0.39 |
| | Number of open patches | −0.02 | −0.13 | 0.08 | 0.34 |
| Climate | Maximum temperature | 0.03 | −1.45 | 1.34 | 0.48 |
| | Precipitation | −0.02 | −0.94 | 0.97 | 0.47 |
| Interactions | Large tree density × perc. ponderosa | 0.01 | −0.10 | 0.13 | 0.41 |
| | Small tree density × perc. ponderosa | −0.01 | −0.12 | 0.10 | 0.44 |
| | Small tree density × maximum temperature | −0.10 | −1.22 | 1.13 | 0.42 |
| | Large tree density × maximum temperature | 0.04 | −0.99 | 1.15 | 0.47 |
| | Percent of landscape harvested × percent burned | 0.02 | −0.10 | 0.14 | 0.35 |
| | Temperature × precipitation | −0.52 | −3.71 | 2.38 | 0.35 |

*Bolded values indicate significant effects (Bayesian p-value < 0.05).

### 3.4. Egg and nestling survival models

The egg survival model explained 76% of the variance in egg survival (Appendix S3, Fig. S7, Panel B). Based on the graphical posterior predictive check, the model predicted slightly larger mean estimates of the number of eggs surviving to young than the observed data (Appendix S3, Fig. S7, Panel A). Overall median estimated egg survival was 44% (95% BCI = [18%, 70%]). Egg survival was higher in sites associated with stand-scale burning compared to unmanaged locations ($\hat{\beta}_{TrtID=Burn}$ = 1.85; 95% BCI = [0.02, 4.01], Fig. 5, Panel A). Egg survival was also higher in sites with higher landscape-scale forest patch size coefficient of variation ($\hat{\beta}_{ForestCV}$ = 0.49; 95% BCI = [0.00, 1.06], Fig. 5, Panel B). Monthly maximum temperature had a negative effect on egg survival ($\hat{\beta}_{Tmax}$ = -0.86; 95% BCI = [-1.60, −0.11], Fig. 5, Panel C), whereas monthly cumulative precipitation had a positive effect ($\hat{\beta}_{PPT}$ = 0.49; 95% BCI = [0.02, 1.00], Fig. 5, Panel D). Aside from these effects, no landscape-scale forest management, nest attributes, or local-scale vegetation covariates influenced egg survival. Results for all model covariates can be found in Table 3. Of the continuous covariates, maximum temperature had the largest effect on egg survival, followed by a relatively similar effect of precipitation and forest patch size coefficient of variation (Table 3). More variation was attributed to the random effect of transect ($\hat{\sigma}^2_{transect}$ = 1.44; 95% BCI = [0.90, 2.15]) compared to year ($\hat{\sigma}^2_{year}$ = 0.18; 95% BCI = [0.89, 2.18]). CFLRP location did not explain a significant amount of residual variance (1.0%), however, there were clear pair-wise differences in transect-level error terms between the Fremont-Winema and Payette National Forest sites (higher error in Payette; difference = 0.81; p-value = 0.01) and the Fremont-Winema and Malheur Forest sites (higher error in Malheur; difference = 0.79; p-value = 0.04; Appendix S3, Fig. S11).

The nestling survival model explained 76% of the variance in nestling survival (Appendix S3, Fig. S8, Panel B). The model predicted similar mean estimates of the number of young surviving to fledging as the observed data (Appendix S3, Fig. S8, Panel A). Overall median nestling survival was 73% (95% BCI = [48%, 89%]). Nest sites in areas associated with a combination of stand-scale harvest and burn had higher nestling survival compared to unmanaged sites ($\hat{\beta}_{TrtID=HarvestBurn}$ = 1.90; 95% BCI = [0.10, 3.92]; Fig. 6, Panel A). At the landscape scale, nestling survival decreased as the percent of burned landscape increased ($\hat{\beta}_{PercBu}$ = -1.43; 95% BCI = [-2.29, −0.62], Fig. 6, Panel B). Nestling survival was higher in western juniper compared to ponderosa pine (*Juniperus occidentalis;* $\hat{\beta}_{Species=JUOC}$ = 1.35; 95% BCI = [0.03, 2.76]), lower in true fir compared to ponderosa pine (*Abies* spp.; $\hat{\beta}_{Species=ABIES}$ = -7.52; 95% BCI = [–22.95, 0.04]) and not clearly different in aspen or Douglas-fir (Fig. 6, Panel C; effects estimates are summarized in Table 4). Nestling survival increased with nest height ($\hat{\beta}_{Ht}$ = 0.28; 95% BCI = [-0.05, 0.62], Fig. 6, Panel D) and decreased with later nest initiation dates ($\hat{\beta}_{Init}$ = -0.40; 95% BCI = [-0.79, 0.00], Fig. 6, Panel E).

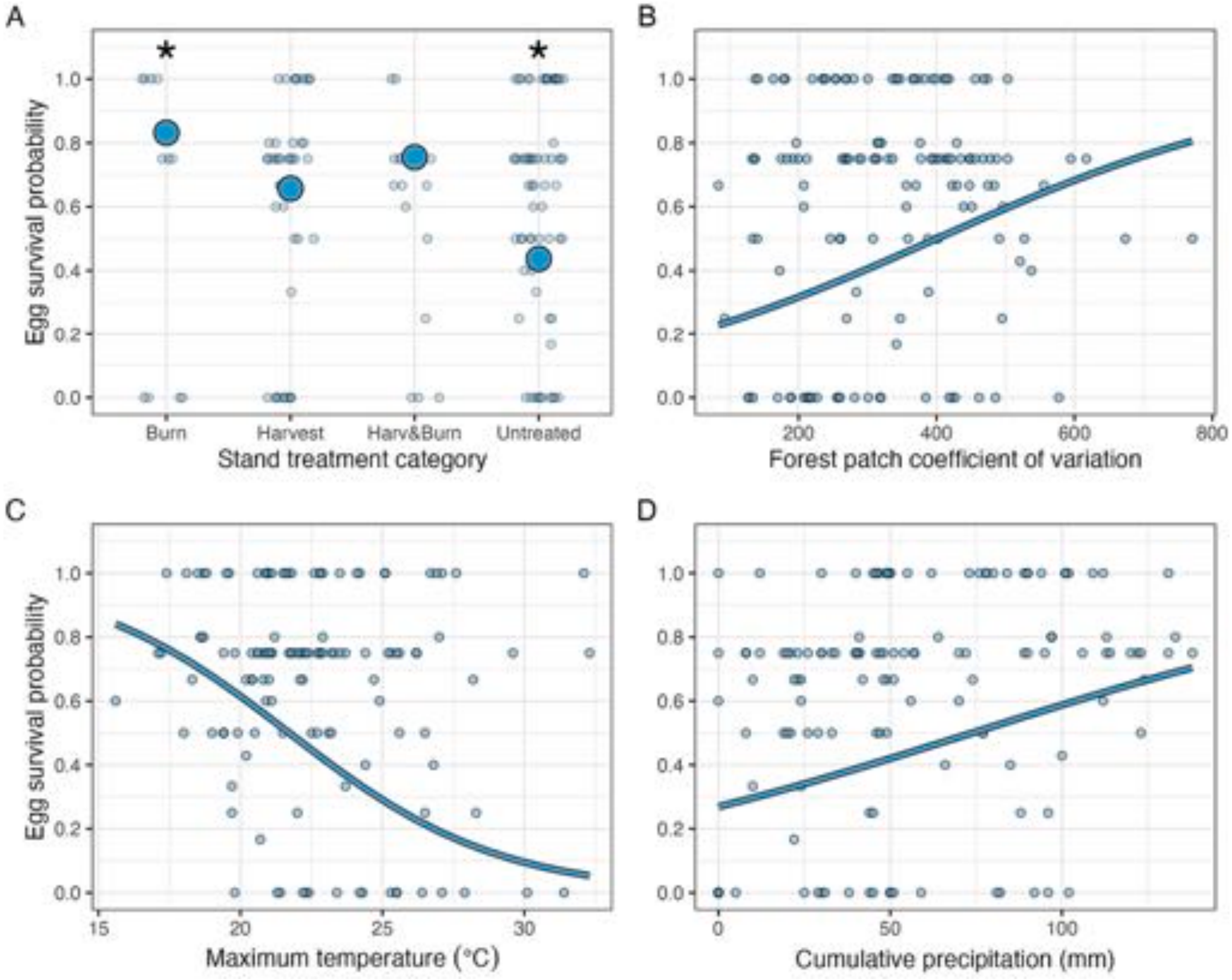

**Fig. 5.** Marginal effects of the most important variables shaping egg survival for white-headed woodpeckers in the three CFLRP locations. These variables include A) nest site forest management category (asterisks indicate difference between baseline "untreated" and "burned" categories;, B) variation in forested patches at the landscape scale, C) maximum temperature, and D) cumulative precipitation.

**Table 3**
Egg survival model results, showing covariates included in the model, and the posterior estimates (median, 95% Bayesian credible interval [BCI] limits, and Bayesian p-value) for each covariate main effect or interaction effect.

| *Covariate category* | *Covariate* | *Median* | *Lower BCI* | *Upper BCI* | *Bayesian p-value* |
|---|---|---|---|---|---|
| Stand-scale management | Treatment type: Harvest | 0.90 | −0.28 | 2.18 | 0.07 |
| | **Treatment type: Burn** | **1.85** | **0.02** | **4.01** | **0.02** * |
| | Treatment type: Harvest&Burn | 1.38 | −0.67 | 3.57 | 0.09 |
| Landscape-scale management | Landscape perc. Burned | −0.43 | −1.22 | 0.30 | 0.13 |
| | Landscape perc. Harvested | −0.41 | −1.01 | 0.16 | 0.08 |
| Nest attributes | Nest tree species: Aspen | −0.69 | −2.22 | 0.92 | 0.19 |
| | Nest tree species: Juniper | −0.62 | −2.03 | 0.82 | 0.19 |
| | Nest tree species: Douglas-Fir | 0.71 | −0.85 | 2.42 | 0.19 |
| | Nest height | −0.04 | −0.36 | 0.27 | 0.39 |
| | Nest orientation | −0.14 | −0.48 | 0.18 | 0.20 |
| | Nest initiation date | −0.02 | −0.64 | 0.56 | 0.48 |
| Local-scale forest vegetation | Large tree density | 0.13 | −0.22 | 0.49 | 0.24 |
| | Small tree density | −0.11 | −0.46 | 0.23 | 0.27 |
| | Percent ponderosa forest | −0.23 | −0.69 | 0.21 | 0.15 |
| Landscape-scale forest vegetation | Percent forested landscape | −0.18 | −0.83 | 0.42 | 0.28 |
| | Total number forest patches | 0.03 | −0.39 | 0.45 | 0.45 |
| | **Forest patch size CV** | **0.49** | **0.00** | **1.06** | **0.03** * |
| | Contagion Index | 0.03 | −0.54 | 0.60 | 0.45 |
| | Landscape Patch Index | 0.05 | −0.56 | 0.67 | 0.43 |
| Climate | **Maximum temperature** | **−0.86** | **−1.60** | **−0.11** | **0.01** ** |
| | Maximum temperature$^2$ | 0.19 | −0.09 | 0.46 | 0.09 |
| | **Precipitation** | **0.49** | **0.02** | **1.00** | **0.02** * |
| | Precipitation$^2$ | −0.13 | −0.56 | 0.33 | 0.28 |
| Interactions | Small trees × Percent ponderosa | 0.03 | −0.36 | 0.43 | 0.43 |
| | Large trees × temperature | −0.01 | −0.40 | 0.37 | 0.48 |
| | Small trees × temperature | −0.12 | −0.47 | 0.25 | 0.26 |
| | Perc. harvest × perc. burned | 0.20 | −0.24 | 0.65 | 0.18 |
| | Temperature × precipitation | −0.18 | −0.74 | 0.37 | 0.26 |

*Bolded values indicate significant effects (Bayesian p-value $< 0.05$).

No local- or landscape-scale forest vegetation features influenced nestling survival. Monthly maximum temperature had a positive effect on nestling survival ($\widehat{\beta}_{\text{Tmax}} = 1.11$; 95% BCI = [0.72, 1.54]), accompanied by a negative quadratic term ($\widehat{\beta}_{\text{Tmax2}} = -0.29$; 95% BCI = [-0.60, 0.03], Fig. 6, Panel F), indicating an "optimal" monthly maximum temperature of 32.41 °C. Nestling survival was higher with increased cumulative precipitation ($\widehat{\beta}_{\text{PPT}} = 0.29$; 95% BCI = [-0.05, 0.84], Fig. 6, Panel G). For the continuous covariates, maximum temperature was the most important, followed by percent of landscape burned, nest initiation date, the quadratic effect of maximum temperature, precipitation, and nest height (Table 4). More variation was attributed to transect ($\widehat{\sigma}^2_{\text{transect}} = 1.98$; 95% BCI = [1.35, 2.86]) compared to year ($\widehat{\sigma}^2_{\text{year}} = 0.76$; 95% BCI = [0.33, 1.69]). Forest location did not explain a significant amount of residual variance (0.6% residual variance, Appendix S3, Fig. S12).

### 3.5. *Comparison across nesting stages*

We highlight patterns among covariate effects of the three models with ecologically significant results (nest initiation date, egg survival, and nestling survival). Although each of the models had a distinct set of important covariates, some patterns were consistent across all three. When comparing the two survival models, which had the same number of candidate variables, more variables influenced nestling survival (7) than egg survival (4).

### 3.6. *Stand- and landscape-scale management covariates*

Both egg and nestling survival were influenced by management at the stand scale. Egg survival was higher in burned stands than untreated stands (Fig. 5, Panel A). Nestling survival was higher in harvested and burned stands compared to untreated stands (Fig. 6, Panel A). Nest initiation date and nestling survival were also influenced by landscape variables related to management. Nest initiation occurred later with increased percentage of landscape harvested (Fig. 4, Panel A) while nestling survival was lower with increased percentage of landscape burned (Fig. 6, Panel B).

### 3.7. *Nest tree-, local-, and landscape-scale covariates*

Egg survival increased as the forest patch size coefficient of variation increased at the landscape scale (Fig. 5, Panel B). Forest vegetation covariates at the smallest spatial scale (nest attributes) were only important to nestling survival. Nestling survival decreased with later nest initiation date. Nestling survival increased with nest height. Nestling survival was lower for nests occurring in true fir and higher for nests occurring in western juniper compared to ponderosa pine (Fig. 6, Panels C-E).

### 3.8. *Climate covariates*

Climate played a role in nest initiation date, egg survival, and nestling survival. Maximum temperature significantly influenced all three responses. Nests initiated earlier with higher antecedent maximum temperature, being driven by temperature conditions in all months from the previous nesting season, with August and September having a slightly higher importance (Fig. 4, Panel C). The relationship between maximum temperature and survival varied by stage: higher temperatures led to lower egg survival (Fig. 5, Panel C), and temperature had a quadratic effect on nestling survival with mostly a positive relationship in the range of values observed in our dataset but with an optimal temperature of ~32° C after which nestling survival decreased (Fig. 6, Panel F). Increased cumulative precipitation led to increased egg and nestling survival (Fig. 5, Panel 4; Fig. 6, Panel G).

## 4. Discussion

In this study, we demonstrated that forest restoration, forest vegetation, and climate variables at multiple spatial and temporal scales influenced the nesting ecology of white-headed woodpeckers and that responses differ depending on nesting stage. While the specific predictor variables that we focused on differed among the four responses (nest

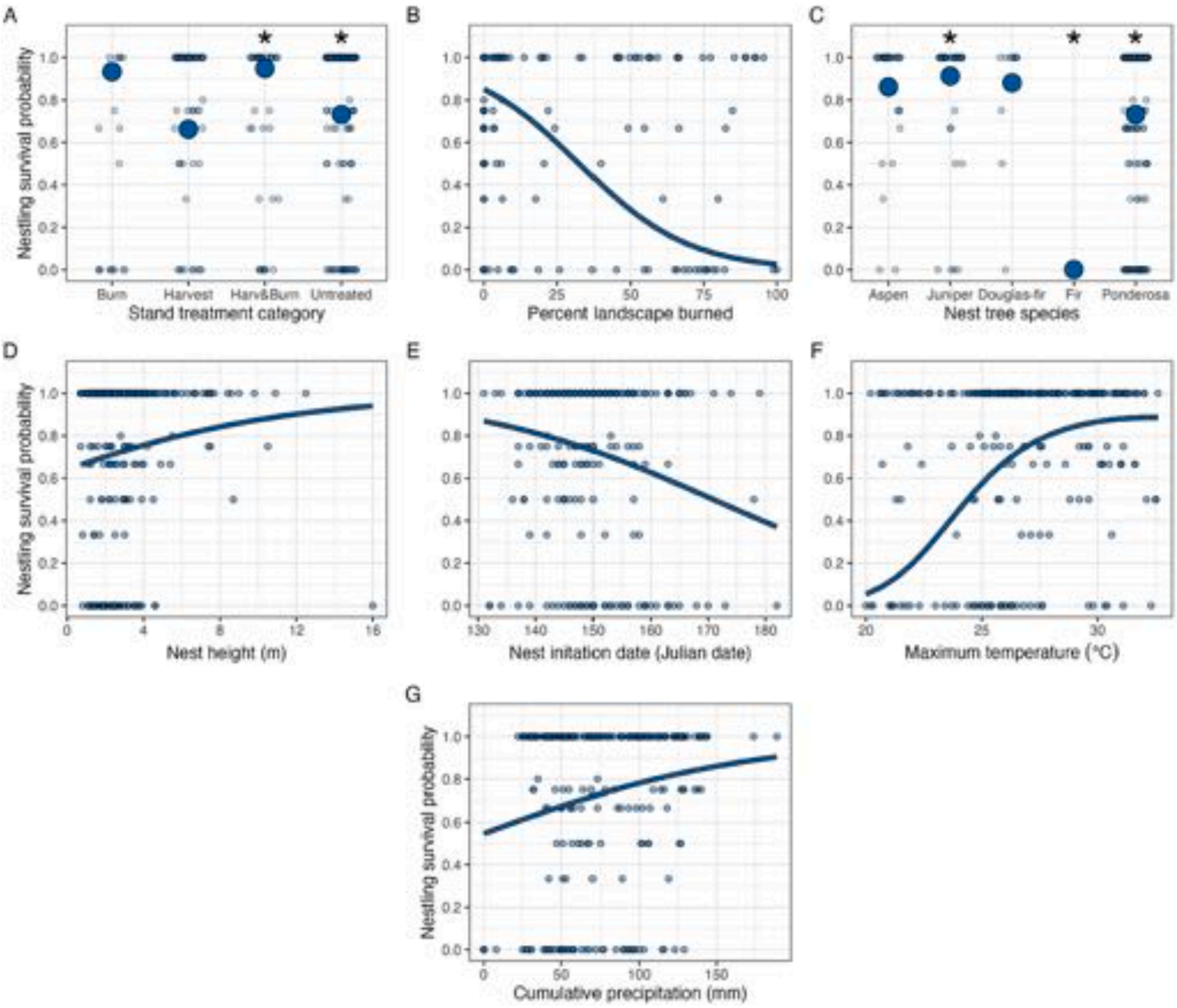

**Fig. 6.** Marginal effects of the most important variables shaping nestling survival model for white-headed woodpecker in the three CFLRP locations. These variables include A) nest site forest management (asterisks indicate difference between baseline "untreated" and "harvested and burned" categories), B) the percent of the landscape managed with burning, C) nest tree species (asterisks indicate difference between baseline "ponderosa" and "true fir" and "juniper" categories), D) nest height, E) nest initiation date, F) maximum temperature, and G) cumulative precipitation (G).

initiation date, egg production, egg survival, and nestling survival), all models included predictors that captured forest management, vegetation, and climate at appropriate spatial scales. Overall, no factors affected egg production, but nest initiation date and egg and nestling survival were all influenced by aspects of the forest management regime and climate. However, the importance and directional effect of different factors often depended on nesting stage. For example, maximum temperature decreased egg survival but generally increased nestling survival (the relationship was quadratic, though, along most of the observed data range, temperature had a positive effect). Importantly, there were shared and different factors for each stage, suggesting that forest restoration, habitat characteristics, and climate impose different limitations depending on season or life stage (Stillman et al., 2019, Purcell and McGregor, 2021). In addition, nestling survival was shaped by the restoration regime with contrasting effects depending on spatial scale. While restoration that reduced tree density and included burning had a positive effect at the stand scale, at the landscape scale, burning activities had negative effects on nestling survival. These differential outcomes highlight that examining the effects of multiple spatial scales on multiple life stages leads to a more nuanced understanding of how forest management, including type and extent, influences nesting biology throughout the breeding season (Shew et al., 2019).

## 4.1. *Management has different effects based on life stage and spatial scale*

### 4.1.1. *Management and nest initiation date*

Nest initiation date was influenced by the spatial extent of the forest management activity, with nests initiating later into the season as the extent of the landscape harvested increased. This landscape effect may be reflective of relatively warm winters, which occur in the study region. In regions with warm winters, more open areas retain snow longer than denser forest (Lundquist et al., 2013). Adults choosing to nest may use a melting snowpack as an indication of the onset of spring, thus initiating nests later in areas where snow remains longer (harvested areas). Later nest initiation date decreased survival of nestlings later in the season, so management that creates large, open, or less dense forested areas had potentially negative implications for later population stages.

### 4.1.2. *Management and egg and nestling survival*

Multiple management activities increased both egg and nestling survival at the stand scale; egg survival increased in burned stands, and nestling survival increased in stands with a combination of burn and harvest (Figs. 5 and 6). Thus, the act of management itself may confer some benefit for nests, including a reduction in nest predation or by creating a more favorable nest microclimate (Davis et al., 2019, Purcell and McGregor, 2021). However, for nestling survival, as the extent of

**Table 4**

Nestling survival model results, showing covariates included in the model, and the posterior estimates (median, 95% Bayesian credible interval [BCI] limits, and Bayesian p-value) for each covariate main effect or interaction effect.

| Covariate category | Covariate | Median | Lower BCI | Upper BCI | Bayesian p-value |
|---|---|---|---|---|---|
| Stand-scale management | Treatment type: Harvest | −0.33 | −1.53 | 0.84 | 0.29 |
| | Treatment type: Burn | 1.63 | −0.42 | 3.87 | 0.06 |
| | **Treatment type: Harvest&Burn** | **1.90** | **0.10** | **3.92** | **0.02** * |
| Landscape -scale management | **Perc. landscape burned** | **−1.43** | **−2.29** | **−0.62** | **0.00** ** |
| | Perc. landscape harvested | 0.17 | −0.42 | 0.76 | 0.28 |
| Nest attributes | Nest tree species: Aspen | 0.83 | −0.69 | 2.37 | 0.14 |
| | **Nest tree species: Juniper** | **1.35** | **0.03** | **2.76** | **0.02** * |
| | Nest tree species: Douglas Fir | 1.00 | −0.40 | 2.61 | 0.08 |
| | **Nest tree species: Fir** | **−7.52** | **−22.95** | **0.04** | **0.03** * |
| | **Nest height** | **0.28** | **−0.05** | **0.62** | **0.05** * |
| | Nest orientation | −0.18 | −0.48 | 0.10 | 0.11 |
| | **Nest initiation date** | **−0.40** | **−0.79** | **0.00** | **0.03** * |
| Local-scale forest vegetation | Large tree density | −0.08 | −0.48 | 0.33 | 0.35 |
| | Small tree density | −0.21 | −0.52 | 0.11 | 0.10 |
| | Percent ponderosa forest | −0.17 | −0.61 | 0.24 | 0.21 |
| Landscape-scale forest vegetation | Percent forested landscape | 0.18 | −0.38 | 0.78 | 0.26 |
| | Total number of forest patches | 0.12 | −0.33 | 0.56 | 0.30 |
| | Forest patch size CV | 0.11 | −0.29 | 0.53 | 0.29 |
| | Contagion | 0.12 | −0.39 | 0.61 | 0.32 |
| | Largest Patch Index | 0.22 | −0.25 | 0.68 | 0.18 |
| Climate | **Maximum temperature** | **1.11** | **0.72** | **1.54** | **0.00** ** |
| | **Maximum temperature$^2$** | **−0.29** | **−0.60** | **0.03** | **0.04** * |
| | **Precipitation** | **0.39** | **−0.05** | **0.84** | **0.04** * |
| | Precipitation$^2$ | 0.25 | −0.07 | 0.60 | 0.06 |
| Interactions | Small trees × percent ponderosa | 0.10 | −0.23 | 0.45 | 0.27 |
| | Large trees × percent ponderosa | −0.14 | −0.57 | 0.25 | 0.24 |
| | Large trees × temperature | 0.14 | −0.20 | 0.48 | 0.21 |
| | Perc harvest × perc. burned | 0.28 | −0.16 | 0.76 | 0.11 |
| | Temperature × precipitation | 0.07 | −0.29 | 0.48 | 0.35 |

*Bolded values indicate significant effects (Bayesian p-value $< 0.05$).

management activities increased (percent of landscape burned), survival rates decreased. The landscape burn effects match previous work that suggests white-headed woodpecker nesting success is greatest in a landscape with a mosaic of burned and unburned patches (e.g., Wightman et al., 2010, Hollenbeck et al., 2011). This pattern may arise if burned conditions lead to more sparse food sources, making adults forage farther from the nest to find food and putting nests at risk of predation or weather extremes (Kehoe, 2017). The seemingly divergent patterns of management effects at the stand and landscape scales highlight the importance of considering spatial scale of management actions when considering effects on wildlife (Vergara and Armesto, 2009, Shew et al., 2019). In addition, the landscape-level treatment variables also incorporated temporal aspects, because we summarized burning that had occurred over the previous 10 years; thus, these burn effects could also be linked to the frequency of prescribed burning disturbance in addition to extent.

#### 4.1.3. *Forest vegetation variables shaped by management influence nestling survival*

In addition to the effects of management activities themselves, management alters multiple local and landscape-scale vegetation features and thus shapes nesting ecology of white-headed woodpeckers through the effects of vegetation structure and composition. Specifically, egg survival was positively influenced by the coefficient of variation of the size of forest patches. This metric describes the variation in patch sizes on the landscape: higher values relate to a greater degree of difference among patch sizes. Landscape patchiness is a known driver of white-headed woodpecker nesting ecology (Hollenbeck et al., 2011), where greater patchiness is associated with more variables sizes of open and closed forested areas, creating a beneficial combination of open areas for nesting and forested areas for adult foraging.

### 4.2. *Past and concurrent climate shape nesting ecology across stages*

#### 4.2.1. *Climate impacts on nest initiation*

Climate, both past and present, shapes nesting ecology across the nesting season. Nest initiation date responded to antecedent climate, which is likely a proxy for the foraging resources that adults access prior to the nesting season (i.e., after the previous summer into the current spring). Because climate conditions in the previous August and September emerged as most influential, this suggests that resource availability right after the previous nesting season is an important determinant of when adults initiate nesting the following year. White-headed woodpeckers rely on a combination of invertebrate and pine cone resources, but depend more on invertebrates during the nesting season (Dixon, 1995, Garrett et al., 1996) and more on green cones during the fledging season (Lorenz et al., 2016). Warmer August and September conditions may trigger the green cones that white-headed woodpeckers rely on for food in this season to ripen faster, or for invertebrates in these cones to mature faster, thus providing a pulse of food that increases fitness and triggers earlier nest initiation the following year. The only slightly increased importance of August and September of the previous year compared to all other previous months may be due to the fact that cone production in ponderosa pine varies from year to year, likely due in part to climatic factors (Krannitz and Duralia, 2023).

#### 4.2.2. *Climate impacts on egg and nestling survival*

Studies focusing on white-headed woodpecker nest survival across the entire nesting season (e.g. Wightman et al., 2010, Hollenbeck et al. 2011, Purcell and McGregor, 2021) have shown an increase in survival with increased maximum temperature during the nesting season (Hollenbeck et al., 2011). In our study, however, egg survival decreased with maximum temperature during the early nesting season, and nestling survival peaked at an “optimal” maximum temperature (e.g., quadratic relationship in the model) later in the nesting season. This suggests that while the overall effect of temperature may be positive for nest outcomes, this effect is more nuanced across nesting stages. Perhaps eggs survive best when adults are not heat-stressed while incubating eggs early in the season. In contrast, nestlings survive at an optimal temperature where adults can find insect prey (Conway and Martin, 2000, Wiebe, 2001, DuRant et al., 2013, Öberg et al., 2015) and nestlings can maintain homeostasis while unattended in nests. Increased precipitation increased both egg and nestling survival. This positive effect of precipitation likely reflects the need for sufficiently wet conditions to support invertebrate prey, without being overly wet (too rainy) to prevent adults from leaving the nest cavity to forage or for invertebrates to cease activity. We note, however, that the climate data we used for this project were at a monthly resolution, yet the process of transitioning from egg to nestling to fledgling can happen within weeks to months. Thus, while we captured average climate effects, finer-resolution data may provide more accurate insights.

#### 4.2.3. *Why is a multi-stage approach important?*

This study provides a novel way to monitor the effects of landscape-scale management on a focal wildlife species. Specifically, this study highlights that examining bird responses across seasons and life stages gives a broader picture of management effects on wildlife. If we only focused on one season or stage, we may miss the nuanced effects of management or other factors that vary across life stages. A clear example of this, as revealed in this study, is that we observed a change in nest initiation date despite no clear changes in egg production. For many birds, and woodpeckers in particular, clutch size remains fairly constant despite variable nesting suitability (Wiktander et al., 2001, Rossmanith et al., 2007, Edworthy et al., 2011). Even if adult birds lay the same number of eggs, when adults choose to start nesting has consequences for later stages, including the negative effect of later initiation dates on nestling survival (Rossmanith et al., 2007, Wiebe and Gerstmar, 2010). Additionally, the number of factors shaping nesting ecology increased from the start to the end of the nesting season (i.e., more factors shaped nestling survival than egg survival), a trend that would not be observed without a multi-stage approach. These differences suggest that nestling survival is vulnerable to more environmental conditions than egg survival, potentially because nestlings are left unattended by adults more often than eggs (Chazarreta et al., 2011). Thus, factors that shape nest predation risk and nestling physiology become more important to nesting success as nests age (Visser and Ricklefs, 1993, Weathers et al., 2000). Just as different wildlife guilds respond differently to management actions (e.g., Shew et al., 2019, Pavlacky et al., 2022), so does management influence various life stages in different ways. Thus, management programs may need to consider collecting data across multiple life stages for focal species to better understand population responses.

#### 4.2.4. *Management recommendations*

The variable responses across the nesting season to forest management actions suggest that the impact (positive or negative) of different management actions can vary within a wildlife population, across different life stages and seasons. This suggests that managers consider the type and extent of management actions and how they relate to various life stages. Overwhelmingly, the response to forest management and resulting landscape conditions was positive or neutral across nesting stages (except for landscape-scale burning for nestling survival). Combining these results with previous work suggests, in general, that management prioritizing patches of open and closed canopy is best for white-headed woodpecker nesting ecology (Wightman et al., 2010, Hollenbeck et al., 2011, Latif et al., 2015, Latif et al., 2020a). Our results suggest that having variable forest patch sizes around nests is conducive to egg survival, though we could not directly evaluate the forest patch size that is best for white-headed woodpeckers. It is important to note that even negative effects of forest treatment on nesting ecology of white-headed woodpeckers may be transitory (Tingley et al., 2023). Ongoing wildfire activity in the western United States is demonstrating the efficacy of prescribed burning prior to large, high-severity wildfire for maintaining forest patches (Latif et al., 2021, 2021, Taylor et al., 2022). Thus, decisions to manage dry mixed-conifer forests in the face of wildfire may have to balance short-term versus long-term impacts. Specifically, while forest management may pose short-term risks to wildlife populations, forest management may be crucial to maintaining any wildlife habitat following wildfire (Prather et al., 2008).

#### 4.2.5. *Next steps*

Extending this multi-stage approach beyond one focal species provides opportunities to address new questions relevant to management and wildlife. For example, examination of other aspects of the management regime, including frequency, configuration, and interval of management through experimental studies may be crucial for making management considerations that are adaptive to the seasonal needs of wildlife (e.g., altering management seasons or the frequency at which management occurs; Shew et al., 2019). Other variables influence when birds nest and how successful they are, including the age or experience level of nesting adults (Lozano et al., 1996). This may be especially important for our model of nest initiation date because more experienced adults are likely to time their nesting behavior more appropriately to conditions that confer nesting success (Lozano et al., 1996). We examined the effects of management on nesting life stages independently. A next step is to build a cohesive model of how all these different life stages interact and contribute to population persistence. Combining nesting data with other data streams (e.g., adult occupancy) to understand population dynamics could be facilitated by approaches such as integrated population models (Schaub and Abadi, 2011, Zipkin and Saunders, 2018, Riecke et al., 2019). Such models may help to inform where population bottlenecks occur (e.g., what stages are most vulnerable to perturbations) and allow for simulation and planning of different management scenarios and their impacts on population persistence (Saunders et al., 2019).

## 5. Conclusion

As landscape-scale restoration efforts continue to grow in number and extent, documenting the effects on not just forest vegetation, but also on the wildlife associated with these forests, is imperative for understanding how management influences forest ecosystems. While there has been an emphasis on focal species responses, a growing number of studies are highlighting the effects of landscape-scale restoration for communities of organisms (Phalan et al., 2019, Shew et al., 2019, Pavlacky et al., 2022, Latif et al., 2022). However, our study demonstrates that it is equally important to look within species (across different life stages) as well as across species to understand the nuanced ways in which forest management shapes wildlife biodiversity (e.g., Stillman et al., 2019). Management of large landscapes is likely to have complex and differing outcomes for forest vegetation and wildlife and considering multi-stage, multi-scale effects will help refine management and develop monitoring programs that meet the needs of ecosystem restoration while effectively capturing ecological outcomes.

## 6. Authors' contributions

All authors conceptualized this study. CC, JD, AM, and VS developed and led field data collection. JD and MW provided data on treatments and landscape variables. CC and AM provided valuable input on the management context of the study. AMtK, KO, and JS developed the analyses. AMtK conducted analyses and led the writing of the manuscript. JD, VS, MW, and JS provided supportive roles in writing the methods section. KO, JS, and MW provided critical feedback on analyses. All authors contributed critically to the editing of the manuscript and gave final approval for publication.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data and code used to generate the analyses for this paper can be found in the Forest Service Research Data Archive (Miller-ter Kuile et al., 2023).

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## Appendix A. Supplementary data

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## References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723.

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P. B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecol. Appl. 12, 1418–1433.

Barton, K. 2020. MuMIn: Multi-Model Inference.

Battaglia, M.A., Gannon, B., Brown, P.M., Fornwalt, P.J., Cheng, A.S., Huckaby, L.S., 2018. Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA. For. Ecol. Manage. 422, 147–160.

Brooks, M., E., K. Kristensen, K. Benthem J. ,van, A. Magnusson, C. Berg W., A. Nielsen, H. Skaug J., M. Mächler, and B. Bolker M. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9:378.

Chazarreta, M.L., Ojeda, V.S., Trejo, A., 2011. Division of labour in parental care in the Magellanic Woodpecker Campephilus magellanicus. J. Ornithol. 152, 231–242.

Ciuzio, E., Hohman, W.L., Martin, B., Smith, M.D., Stephens, S., Strong, A.M., Vercauteren, T., 2013. Opportunities and challenges to implementing bird conservation on private lands: Bird Conservation on Private Land. Wildl. Soc. Bull. 37, 267–277.

Conn, P.B., Johnson, D.S., Williams, P.J., Melin, S.R., Hooten, M.B., 2018. A guide to Bayesian model checking for ecologists. Ecol. Monogr. 88, 526–542.

Conway, C.J., Martin, T.E., 2000. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54, 670–685.

McKay Curtis, S. 2018. mcmcplots: Create Plots from MCMC Output.

Cushman, S.A., McGarigal, K., Neel, M.C., 2008. Parsimony in landscape metrics: Strength, universality, and consistency. Ecol. Ind. 8, 691–703.

Cyphers, L.A., Schultz, C.A., 2019. Policy design to support cross-boundary land management: the example of the Joint Chiefs Landscape Restoration Partnership. Land Use Policy 80, 362–369.

Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E., Abatzoglou, J.T., 2019. Microclimatic buffering in forests of the future: the role of local water balance. Ecography 42, 1–11.

Davis, K. T., M. D. Robles, K. B. Kemp, P. E. Higuera, T. Chapman, K. L. Metlen, J. L. Peeler, K. C. Rodman, T. Woolley, R. N. Addington, B. J. Buma, C. A. Cansler, M. J. Case, B. M. Collins, J. D. Coop, S. Z. Dobrowski, N. S. Gill, C. Haffey, L. B. Harris, B. J. Harvey, R. D. Haugo, M. D. Hurteau, D. Kulakowski, C. E. Littlefield, L. A. McCauley, N. Povak, K. L. Shive, E. Smith, J. T. Stevens, C. S. Stevens-Rumann, A. H. Taylor, A. J. Tepley, D. J. N. Young, R. A. Andrus, M. A. Battaglia, J. K. Berkey, S. U. Busby, A. R. Carlson, M. E. Chambers, E. K. Dodson, D. C. Donato, W. M. Downing, P. J. Fornwalt, J. S. Halofsky, A. Hoffman, A. Holz, J. M. Iniguez, M. A. Krawchuk, M. R. Kreider, A. J. Larson, G. W. Meigs, J. P. Roccaforte, M. T. Rother, H. Safford, M. Schaedel, J. S. Sibold, M. P. Singleton, M. G. Turner, A. K. Urza, K. D. Clark-Wolf, L. Yocom, J. B. Fontaine, and J. L. Campbell. 2023. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. Proceedings of the National Academy of Sciences 120:e2208120120.

Dixon, R., 1995. Ecology of White-Headed Woodpeckers in the Central Oregon Cascades. University of Idaho.

Dorazio, R.M., 2016. Bayesian data analysis in population ecology: motivations, methods, and benefits. Popul. Ecol. 58, 31–44.

Drapeau, P., Villard, M.-A., Leduc, A., Hannon, S.J., 2016. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. Divers. Distrib. 22, 385–399.

Dudley, J.G., Saab, V., 2003. A Field Protocol to Monitor Cavity-Nesting Birds. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

DuRant, S.E., Hopkins, W.A., Hepp, G.R., Walters, J.R., 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds: Incubation temperature and avian offspring phenotype. Biol. Rev. 88, 499–509.

Edworthy, A.B., Drever, M.C., Martin, K., 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. For. Ecol. Manage. 261, 203–210.

ESRI, 2019. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, California, USA.

Fox, J., Hong, J., 2009. Effect displays in *R* for multinomial and proportional-odds logit models: extensions to the **effects** package. J. Stat. Softw. 32.

Garrett, K., Raphael, M.G., Dixon, R.D., 1996. White-headed woodpecker: Picoides albolarvatus. American Ornithologists' Union.

Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Anal. 1, 515–533.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2020. Bayesian Data Analysis.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7.

Grolemund, G., Wickham, H., 2011. Dates and times made easy with lubridate. J. Stat. Softw. 40, 1–25.

Guo, J.S., Hultine, K.R., Koch, G.W., Kropp, H., Ogle, K., 2020. Temporal shifts in iso/anisohydry revealed from daily observations of plant water potential in a dominant desert shrub. New Phytol. 225, 713–726.

Hagmann, R.K., Hessburg, P.F., Prichard, S.J., Povak, N.A., Brown, P.M., Fulé, P.Z., Keane, R.E., Knapp, E.E., Lydersen, J.M., Metlen, K.L., Reilly, M.J., Sánchez Meador, A.J., Stephens, S.L., Stevens, J.T., Taylor, A.H., Yocom, L.L., Battaglia, M.A., Churchill, D.J., Daniels, L.D., Falk, D.A., Henson, P., Johnston, J.D., Krawchuk, M.A., Levine, C.R., Meigs, G.W., Merschel, A.G., North, M.P., Safford, H.D., Swetnam, T. W., Waltz, A.E.M., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecol. Appl. 31.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R., Bearhop, S., 2011. Carry-over effects as drivers of fitness differences in animals: Carry-over effects in animal populations. J. Anim. Ecol. 80, 4–18.

Hartig, F. 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hayward, G.D., Flather, C.H., Rowland, M.M., Terney, R., Mellen-McLean, K., McCarthy, C., Boyce, D.A., 2016. Applying the 2012 Planning Rule to conserve species: A practitioner's reference. USDA Forest Service, Washington, D.C.

Heinze, G., Wallisch, C., Dunkler, D., 2018. Variable selection - A review and recommendations for the practicing statistician. Biom. J. 60, 431–449.

Herrera, C.M., 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology 63, 773–785.

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manage. 211, 117–139.

Hessburg, P.F., Prichard, S.J., Hagmann, R.K., Povak, N.A., Lake, F.K., 2021. Wildfire and climate change adaptation of western North American forests: a case for intentional management. Ecol. Appl. 31, e02432.

Hollenbeck, J.P., Saab, V.A., Frenzel, R.W., 2011. Habitat suitability and nest survival of white-headed woodpeckers in unburned forests of Oregon. J. Wildl. Manag. 75, 1061–1071.

Jones, G.M., Keane, J.J., Gutiérrez, R.J., Peery, M.Z., 2018. Declining old-forest species as a legacy of large trees lost. Divers. Distrib. 24, 341–351.

Jones, G.M., Keyser, A.R., Westerling, A.L., Baldwin, W.J., Keane, J.J., Sawyer, S.C., Clare, J.D., Gutiérrez, R., Peery, M.Z., 2021. Forest restoration limits megafires and supports species conservation under climate change. Front. Ecol. Environ. fee.2450.

Kehoe, A., 2017. Space Use and Foraging Patterns of the White-Headed Woodpecker in Western Idaho. Montana State University, Bozeman, Montana, USA.

Kellner, K. 2021. jagsUI: A Wrapper Around "rjags" to Streamline "JAGS" Analyses.

Knudson, C. 2022. glmm: Genarlized Linear Mixed Models via Monte Carlo Likelihood Approximation.

Kooistra, C., Sinkular, E., Schultz, C., 2022. Characterizing the context and demand for the Us Forest Service's collaborative forest landscape restoration program in 2020. J. For. 120, 64–85.

Kozma, J.M., 2009. Nest-site attributes and reproductive success of white-headed and hairy woodpeckers along the east-slope Cascades of Washington state. In: Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics, pp. 52–61.

Kozma, J.M., Burkett, L.M., Kroll, A.J., Thornton, J., Mathews, N.E., 2017. Factors associated with nest survival of Black-throated Sparrows, desert-breeding nest-site generalists. J. Field Ornithol. 88, 274–287.

Krannitz, P. G., and T. E. Duralia. 2023. cone and seed production in pinus ponderosa: a review.

Kuhn, M. 2022. caret: Classification and Regression Training.

Latif, Q.S., Saab, V.A., Mellen-Mclean, K., Dudley, J.G., 2015. Evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forest: Model Evaluation for White-Headed Woodpeckers. J. Wildl. Manag. 79, 263–273.

Latif, Q.S., Saab, V.A., Dudley, J.G., Markus, A., Mellen-McLean, K., 2020a. Development and evaluation of habitat suitability models for nesting white-headed woodpecker (Dryobates albolarvatus) in burned forest. PLoS One 15, e0233043.

Latif, Q.S., Truex, R.L., Sparks, R.A., Pavlacky, D.C., 2020b. Dry conifer forest restoration benefits Colorado Front Range avian communities. Ecol. Appl. 30.

Latif, Q.S., Saab, V.A., Dudley, J.G., 2021. Prescribed fire limits wildfire severity without altering ecological importance for birds. Fire Ecology 17, 37.

Latif, Q.S., Cannon, J.B., Chabot, E.J., Sparks, R.A., 2022. Simulated treatment effects on bird communities inform landscape-scale dry conifer forest management. Ecol. Appl. 32.

Lenth, R. 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lin Pedersen, T. 2020. patchwork: The Composer of Plots.

Lorenz, T.J., Vierling, K.T., Kozma, J.M., Millard, J.E., 2016. Foraging plasticity by a keystone excavator, the white-headed woodpecker, in managed forests: Are there consequences for productivity? For. Ecol. Manage. 363, 110–119.

Lozano, G.A., Perreault, S., Lemon, R.E., 1996. Age, arrival date and reproductive success of male american redstarts Setophaga ruticilla. J. Avian Biol. 27, 164.

Lundquist, J.D., Dickerson-Lange, S.E., Lutz, J.A., Cristea, N.C., 2013. Lower forest density enhances snow retention in regions with warmer winters: A global framework developed from plot-scale observations and modeling. Water Resour. Res. 49, 6356–6370.

Luneau Jr., M.D., Noel, B.L., 2010. A wireless video camera for viewing tree cavities: Wireless Video Camera for Viewing Cavities. J. Field Ornithol. 81, 176–185.

McGarigal, K., B. J. Marks, S. Cushman, and E. Ene. 2012. FRAGSTATS v4: spatial pattern analysis program for quantifying landscape structure. Page PNW-GTR-351. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Mellen-McLean, K., Saab, V.A., Bresson, B., Wales, B., Markus, A., VanNorman, K., 2015. White-headed Woodpecker Monitoring Strategy. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA. Page 34.

Menz, M.H.M., Dixon, K.W., Hobbs, R.J., 2013. Hurdles and opportunities for landscape-scale restoration. Science 339, 526–527.

Miller-ter Kuile, A., Ogle, K., Cavanaugh, C., Dudley, J., Markus, A., Saab, V., Wright, M., Sanderlin, J., 2023. Data for: Forest management, forest vegetation, and climate influence nesting ecology of a focal bird species in the western USA. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2023-0053.

Milligan, M.C., McNew, L.B., 2022. Evaluating the cumulative effects of livestock grazing on wildlife with an integrated population model. Front. Ecol. Evol. 10, 818050.

Muller, K. 2020. here: A simpler way to find your files. R.

Öberg, M., Arlt, D., Pärt, T., Laugen, A.T., Eggers, S., Low, M., 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. Ecol. Evol. 5, 345–356.

Ogle, K., Barber, J.J., 2020. Ensuring identifiability in hierarchical mixed effects Bayesian models. Ecol. Appl. 30.

Ogle, K., Barber, J., Sartor, K., 2013. Feedback and modularization in a bayesian meta–analysis of tree traits affecting forest dynamics. Bayesian Analysis 8.

Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E., Loik, M.E., Tissue, D.T., 2015. Quantifying ecological memory in plant and ecosystem processes. Ecol. Lett. 18, 221–235.

Ott, J.E., Kilkenny, F.F., Jain, T.B., 2023. Fuel treatment effectiveness at the landscape scale: a systematic review of simulation studies comparing treatment scenarios in North America. Fire Ecol. 19, 10.

Pasinelli, G., 2001. Breeding performance of the middle spotted woodpecker Dendrocopos medius in relation to weather and territory quality. Ardea 89, 353–361.

Patrick, L.D., Ogle, K., Bell, C.W., Zak, J., Tissue, D., 2009. Physiological responses of two contrasting desert plant species to precipitation variability are differentially regulated by soil moisture and nitrogen dynamics. Glob. Chang. Biol. 15, 1214–1229.

Pavlacky, D.C., Green, A.W., George, T.L., Iovanna, R., Bartuszevige, A.M., Correll, M.D., Panjabi, A.O., Ryder, T.B., 2022. Landscape-scale conservation mitigates the biodiversity loss of grassland birds. Ecol. Appl. 32.

Peltier, D.M.P., Anderegg, W.R.L., Guo, J.S., Ogle, K., 2022. Contemporary tree growth shows altered climate memory. Ecol. Lett. 25, 2663–2674.

Phalan, B. T., J. M. Northrup, Z. Yang, R. L. Deal, J. S. Rousseau, T. A. Spies, and M. G. Betts. 2019. Impacts of the Northwest Forest Plan on forest composition and bird populations. Proceedings of the National Academy of Sciences 116:3322–3327.

Plummer, M., Best, N., Cowles, K., Vines, K., 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6, 7–11.

Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling.

Prather, J.W., Noss, R.F., Sisk, T.D., 2008. Real versus perceived conflicts between restoration of ponderosa pine forests and conservation of the Mexican spotted owl. Forest Policy Econ. 10, 140–150.

Prichard, S.J., Hessburg, P.F., Hagmann, R.K., Povak, N.A., Dobrowski, S.Z., Hurteau, M. D., Kane, V.R., Keane, R.E., Kobziar, L.N., Kolden, C.A., North, M., Parks, S.A., Safford, H.D., Stevens, J.T., Yocom, L.L., Churchill, D.J., Gray, R.W., Huffman, D.W., Lake, F.K., Khatri-Chhetri, P., 2021. Adapting western North American forests to climate change and wildfires: 10 common questions. Ecol. Appl. e02433.

Purcell, K.L., McGregor, E.L., 2021. White-headed woodpecker nesting habitat at multiple spatial scales: are habitat preferences adaptive? For. Ecol. Manage. 499, 119606.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raftery, A., Lewis, S.. 1995. Implementing MCMC. Page Markov Chain Monte Carlo in practice.

Raftery, A.E., Lewis, S.M., 1992. One long run with diagnostics: Implementation strategies for Markov Chain Monte Carlo. Stat. Sci. 7, 493–497.

Raphael, M.G., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86, 3–66.

Rich, T.D., Beardmore, C.J., Berlanga, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G. S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Iñigo-Elias, E.E., Kennedy, J.A., Martell, A.M., Panjabi, A.O., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J. S., Will, T.C., 2004. Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornitholoy, Ithaca, NY, USA, pp. 1–40.

Riecke, T.V., Williams, P.J., Behnke, T.L., Gibson, D., Leach, A.G., Sedinger, B.S., Street, P.A., Sedinger, J.S., 2019. Integrated population models: model assumptions and inference. Methods Ecol. Evol. 10, 1072–1082.

Rossmanith, E., Höntsch, K., Blaum, N., Jeltsch, F., 2007. Reproductive success and nestling diet in the Lesser Spotted Woodpecker (Picoides minor): the early bird gets the caterpillar. J. Ornithol. 148, 323–332.

Saab, V.A., Dudley, J., Thompson, W.L., 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106, 20–36.

Saunders, S. P., M. T. Farr, A. D. Wright, C. A. Bahlai, J. W. Ribeiro, S. Rossman, A. L. Sussman, T. W. Arnold, and E. F. Zipkin. 2019. Disentangling data discrepancies with integrated population models. Ecology:e02714.

Savage, M., Mast, J.N., Feddema, J.J., 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Can. J. For. Res. 43, 570–583.

Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 11.

Schloerke, B., D. Cook, J. Larmarange, F. Briatte, M. Marbach, E. Thoen, A. Elberg, and J. Crowley. 2021. GGally: Extensions to "ggplot2.".

Schultz, C.A., Jedd, T., Beam, R.D., 2012. The collaborative forest landscape restoration program: a history and overview of the first projects. J. For. 110, 381–391.

Shew, J.J., Nielsen, C.K., Sparling, D.W., 2019. Finer-scale habitat predicts nest survival in grassland birds more than management and landscape: A multi-scale perspective. J. Appl. Ecol. 56, 929–945.

Stephens, S. L., M. A. Battaglia, D. J. Churchill, B. M. Collins, M. Coppoletta, C. M. Hoffman, J. M. Lydersen, M. P. North, R. A. Parsons, S. M. Ritter, and J. T. Stevens. 2020. Forest Restoration and Fuels Reduction: Convergent or Divergent? BioScience: biaa134.

Stillman, A.N., Siegel, R.B., Wilkerson, R.L., Johnson, M., Tingley, M.W., 2019. Age-dependent habitat relationships of a burned forest specialist emphasise the role of pyrodiversity in fire management. J. Appl. Ecol. 56, 880–890.

Taylor, A.H., Harris, L.B., Skinner, C.N., 2022. Severity patterns of the 2021 Dixie Fire exemplify the need to increase low-severity fire treatments in California's forests. Environ. Res. Lett. 17, 071002.

Tempel, D.J., Gutiérrez, R.J., Battles, J.J., Fry, D.L., Su, Y., Guo, Q., Reetz, M.J., Whitmore, S.A., Jones, G.M., Collins, B.M., Stephens, S.L., Kelly, M., Berigan, W.J., Peery, M.Z., 2015. Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. Ecosphere 6, art261.

Thomsen, M.S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K.J., Holmer, M., Silliman, B.R., 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr. Comp. Biol. 50, 158–175.

Tingley, M.W., Montgomery, G.A., Wilkerson, R.L., Cluck, D.R., Sawyer, S.C., Siegel, R. B., 2023. Multi-trophic occupancy modeling connects temporal dynamics of woodpeckers and beetle sign following fire. PLoS One 18, e0281687.

USDA, USGS, 2022. LANDFIRE: LANDFIRE Existing Vegetation Canopy Cover layer. Department of Interior, Geological Survey and U.S. Department of Agriculture, U.S.

van Mantgem, P.J., Falk, D.A., Williams, E.C., Das, A.J., Stephenson, N.L., 2018. Pre-fire drought and competition mediate post-fire conifer mortality in western U.S. National Parks. Ecol. Appl. 28, 1730–1739.

Vergara, P.M., Armesto, J.J., 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landsc. Ecol. 24, 25–38.

Visser, G.H., Ricklefs, R.E., 1993. Development of temperature regulation in shorebirds. Physiol. Zool. 66, 771–792.

Wang, T., Hamann, A., Spittlehouse, D., Carroll, C., 2016. Locally Downscaled and spatially customizable climate data for historical and future periods for North America. PLoS One 11, e0156720.

Weathers, W.W., Gerhart, K.L., Hodum, P.J., 2000. Thermoregulation in Antarctic fulmarine petrels. J. Comp. Physiol. 170, 561–572.

Wickham, H., Bryan, J.. 2022. readxl: Read Excel Files.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. J. Open Source Software 4, 1686.

Wickham, H. 2007. Reshaping Data with the reshape Package 21:1–20.

Wiebe, K.L., 2001. Microclimate of tree cavity nests: is it important for reproductive success in northern flickers? Auk 118, 412–421.

Wiebe, K.L., Gerstmar, H., 2010. Influence of spring temperatures and individual traits on reproductive timing and success in a migratory woodpecker. Auk 127, 917–925.

Wightman, C.S., Saab, V.A., Forristal, C., Mellen-McLean, K., Markus, A., 2010. White-headed woodpecker nesting ecology after wildfire. J. Wildl. Manag. 74, 1098–1106.

Wiktander, U., Olsson, O., Nilsson, S.G., 2001. Annual and seasonal reproductive trends in the Lesser Spotted Woodpecker *Dendrocopos minor*. Ibis 143, 72–82.

Wisdom, M. J., R. S. Holthausen, B. C. Wales, C. D. Hargis, V. A. Saab, D. C. Lee, W. J. Hann, T. D. Rich, M. M. Rowland, W. J. Murphy, and M. R. Eames. 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia Basin: broad-scale trends and management implications. General technical report, U.S. Forest Service, Pacific Northwest Research Station.

Zipkin, E.F., Saunders, S.P., 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biol. Conserv. 217, 240–250.