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RESEARCH ARTICLE

The effects of habitat management on populations of a sensitive bird species vary with local climate and habitat

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Abstract

1. Thousands of species across the globe are declining primarily due to habitat loss and conversion. Management actions aimed at habitat restoration can mitigate these effects, though the results are likely to vary across local habitat and climate conditions as well as throughout the lifetime of a species. Thus, it is imperative to examine how local habitat and climate context shape population responses to habitat management.
2. In this study, we develop a modularized Bayesian population model that incorporates management, climate and habitat covariates for three life stages: egg, nestling and adult survival. We apply this modelling approach to three populations of a bird species sensitive to ongoing habitat management (white-headed woodpecker, *Dryobates albolarvatus*) in three landscapes with varying environmental conditions. We examined how management effects vary with local climate and habitat, and how these effects vary across life stages.
3. Of all life stages (egg, nestling and adult survival), habitat management most strongly impacted nestling survival across populations (11%–51% relative importance). However, habitat management was most influential for different life stages across populations, highlighting that local environmental conditions and population status can shape the effects of habitat restoration on species life history.
4. Management actions themselves were relatively unimportant drivers of population growth (5%–10% relative importance); climate conditions were more important (60%–80% relative importance). However, for the population with the habitat conditions most like the historical baseline, these habitat conditions had a relatively greater effect than for the other two populations (30% vs. 9% and 14% relative importance), suggesting that as habitat restoration re-introduces historical conditions, habitat features may more strongly shape populations.
5. *Synthesis and applications.* The effects of management and conservation of populations, species and habitat depend on local environmental context. Species conservation will benefit from examining local factors to help identify high-priority areas for habitat management where these actions will most benefit population persistence.

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KEYWORDS
avian ecology, *Dryobates albolarvatus*, dynamic occupancy models, hierarchical partitioning, integrated population modelling, *Pinus ponderosa*, white-headed woodpecker

1 | INTRODUCTION

Changes in habitat and climate are altering ecosystems across the globe with impacts on populations, communities and ecosystems. (Northrup et al., 2019; Sala et al., 2000). Across ecosystems, habitat loss is the leading cause of population declines for tens of thousands of species (Finn et al., 2023; Jaureguiberry et al., 2022). Active management efforts can restore habitat or environmental conditions to natural or historical ranges and benefit many species (Hobbs et al., 2006; Seidl et al., 2016). These restoration efforts happen on the backdrop of climate conditions that are also changing (Harris et al., 2006). Thus, to fully understand past, current and future population trends for species globally, it is imperative to evaluate the effects of environmental management, climate and habitat in conjunction (Kennedy et al., 2019; Mantyka-pringle et al., 2012).

The effects of habitat management are likely to vary across ontogeny and for populations experiencing different local conditions (Heiland et al., 2022; Komoroske et al., 2014). Species may benefit from habitats, either natural or managed, at one life stage that are population sinks at other stages (e.g. habitats with both high resource availability and predation risk; Stillman et al., 2019). Furthermore, land use change exacerbates climate impacts for species, with stronger effects at thermal range limits (Williams et al., 2022). Climate conditions, such as temperature, may have different effects across life stages (e.g. different magnitudes: Pandori & Sorte, 2019; different directions: Radchuk et al., 2013) and so local habitat conditions, created through management actions or otherwise, may buffer populations facing more climate fluctuations. As a whole, population responses to habitat management will likely be shaped by the emergent effects of local environmental factors acting individually on multiple life stages (Lowe et al., 2021; McDermott Long et al., 2017; Saunders et al., 2018; Zylstra et al., 2021).

To evaluate the benefits of habitat management for declining or at risk species, we need to weigh the relative importance of multiple drivers on local populations (Saunders et al., 2018; Zylstra et al., 2021). This is especially important for species that are vulnerable to ongoing and future decline but that may exist in localized populations that can be supported by active habitat management (e.g. population 'sources': Pulliam, 1988). Examining these patterns through ontogeny may also help in prioritizing management actions, including the type, extent and timing of management that benefit species most with the least disturbance to sensitive life stages (Kalies et al., 2010; Shew et al., 2019). Addressing these questions will support assessments for multiple populations and life stages, especially when combined with modelling approaches that incorporate effects of external drivers (e.g. management, climate and habitat) and propagate uncertainty into values of population trends (Zylstra & Zipkin, 2021). Knowledge gained from such approaches can inform how local context and life stage shape population responses to habitat management and can extend to future management and conservation scenario planning (Oppel et al., 2022; Saunders et al., 2018).

In this study, we examine how local environmental context and life stage shape the responses of three populations of a sensitive bird species (white-headed woodpecker, *Dryobates albolarvatus*) to habitat restoration management actions. White-headed woodpeckers are a species of concern in much of their geographic range (Garrett et al., 1996; Hollenbeck et al., 2011; Latif et al., 2015, 2020; Wightman et al., 2010), their habitats have degraded through fire suppression in the last century (Hagmann et al., 2021), and because of these altered conditions, they will likely face high rates of habitat loss from future high-severity wildfire (Norman et al., 2026). We used 10 years of data from occupancy and nest productivity surveys for each population occurring in actively managed landscapes across a range of underlying climate and habitat conditions (Oregon and Idaho, USA; Figure 1). We developed a modularized Bayesian population modelling approach that allowed us to (a) include management, habitat and climate covariates for each life stage, (b) propagate uncertainty in each of these life stage estimates to population growth and (c) evaluate the relative importance of management to life stage survival and population growth across environmental contexts (Zylstra et al., 2021). Specifically, we asked: what is the relative contribution of habitat management to (1) life stage survival and (2) population growth for populations in different habitat contexts? This work builds understanding for how ecosystem management shapes this species across habitat contexts and provides a modelling framework with which these questions could be asked for other species in other settings.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

In our modularized approach, we first fit individual statistical models to data on vital rates (egg production, egg survival, nestling survival, pre-fledging sex ratios and adult point-level occupancy) for each population, including stage-specific climate, habitat and management covariates. Then, in the second step, we used samples from the posterior distributions of the vital rate parameters from each of these statistical models to parameterize a population model for each population.

We compiled information on nest productivity and adult occupancy, habitat management activities, climate and habitat for three populations of white-headed woodpeckers in Oregon and Idaho, USA. Each population was surveyed for 6–8 years during 2012–2021. The three populations of white-headed woodpeckers occurred in landscapes that have been part of restoration-based management through the USDA Forest Service Collaborative Forest Landscape Restoration

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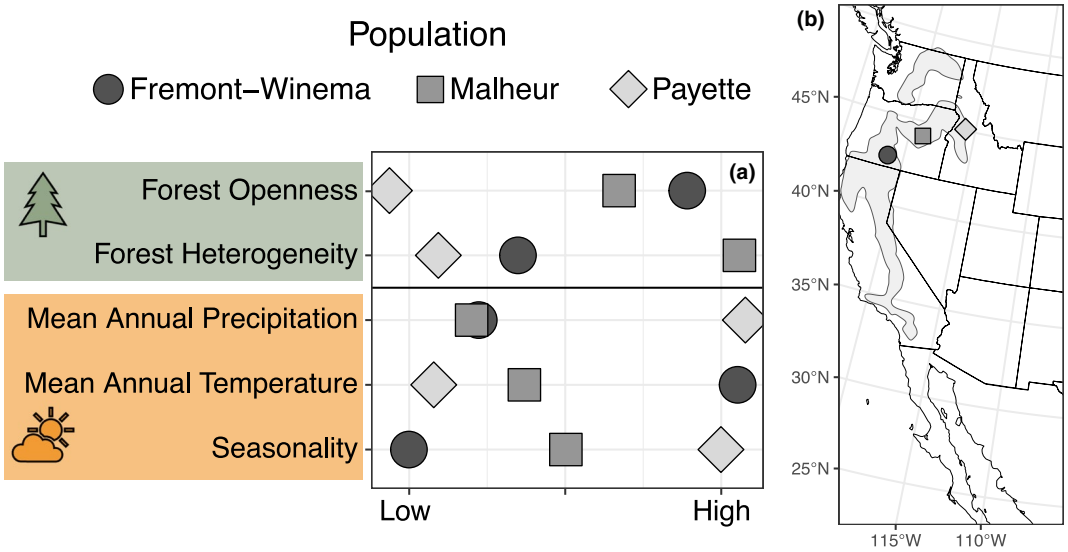


FIGURE 1 Local habitat and climate conditions (a) experienced by each of the three populations of white-headed woodpeckers in our study. Values are standardized across the three populations to show how populations vary in habitat (e.g. forest structure) and climate (e.g. temperature, precipitation and temperature seasonality) conditions. The geographical locations of the three populations are illustrated in (b) with the grey shaded area representing the full species range for the species (eBird Status and Trends, Fink et al., 2025).

Program (CFLRP; https://www.fs.usda.gov/restoration/CFLRP/index.shtml). We refer to the populations throughout as the (1) 'Fremont–Winema' (Lakeview Stewardship Project, Fremont–Winema National Forest, Oregon, USA, 42.2°N, 120.2°W), (2) 'Malheur' (Southern Blues Restoration Coalition, Malheur National Forest, Oregon, USA, 44.0°N, 118.7°W) and (3) 'Payette' (Weiser-Little Salmon Headwaters Project, Payette National Forest, Idaho, USA, 44.8°N, 116.5°W) populations. All three landscapes (and thus, populations) experienced a combination of management actions, including tree removal (primarily trees of 13–51 cm diameter-at-breast-height) followed by prescribed burning. We treated the CFLRP landscapes as representing the range of each 'population' for white-headed woodpeckers because birds were monitored during the nesting season and display high nest site fidelity (Daniels & Walters, 2000; Lorenz et al., 2016). CFLRP landscapes were relatively insulated from other suitable habitat patches within and around each national forest due to a combination of habitat type and land use. Thus, each landscape represents a relatively distinct population range with little or no movement between them. These populations also occur across a range of climate and habitat conditions, which are summarized in Figure 1.

2.2 | Data collection

2.2.1 | Bird datasets

Datasets used to determine population parameters included nesting season occupancy data for adult woodpeckers collected along survey transects and nesting season productivity data, including information on the number of eggs, nestlings and fledglings associated with each nest. We surveyed adult white-headed woodpeckers in each population along 27–30 transects. Transects were 2700 m long, with 10 survey points spaced every 300 m along each transect. Approximately half of the transects were placed in areas that were actively managed (e.g. burning, thinning/harvesting or both) and half in areas that were not actively managed within the timeframe of our study (2012–2021). At each transect point, field technicians performed call-broadcast surveys to determine the presence or absence of adult white-headed woodpeckers (Latif et al., 2015). If technicians observed an adult white-headed woodpecker, they also searched for nests in the surrounding area. Surveyors also revisited nest trees that had been occupied by white-headed woodpeckers in previous years. When surveyors located active nests, they used pole-mounted cameras to observe nest contents. We revisited nests throughout the season and tracked the number of eggs, nestlings and fledglings from each nest. We determined pre-fledgling sex ratios using colour photograph and video camera data collected during nest visits. Numbers of female and male nestlings were determined for each nest from the number of red feathers on each nestling's pileum, males having noticeably more than females (J. Dudley unpublished data). All handling and monitoring of white-headed woodpeckers complied with Institutional Animal Care and Use Committee guidelines (Montana State University Protocol No. 2014-46), the state of Idaho (Permit 950228) and USGS Bird Banding Laboratory (Permit 22607). We worked directly in partnership with biologists, silviculturists and natural resource specialists representing each national forest and did not require additional permits or licences to implement our study.

2.2.2 | Environmental covariates

For nest stages, we used previously published information on covariates that shape egg number, egg survival and nestling survival (Miller-ter

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Kuile et al., 2023). This study examined the relationships between each of these nesting stages and a set of covariates for each nest location that captured ecological variables related to physiology, foraging and habitat risk (e.g. nest predation risk) at multiple spatial scales. In summary, white-headed woodpeckers lay four eggs on average, regardless of other factors (covariates). However, egg survival is shaped by stand-scale (2.25 ha) prescribed burning, variation in the size of closed-forest (40%–100% canopy cover) patches at the landscape scale (314 ha), average monthly maximum temperature and cumulative precipitation during the period when nests have eggs. Nestling survival is shaped by stand-scale prescribed burning and thinning, landscape-scale percent burned, nest tree species, nest height, nest initiation date, average monthly maximum temperature and cumulative precipitation during the period when nests have nestlings (Figure 2).

In addition to these known covariates for nesting stages, we also compiled a set of landscape-scale (1 km radius, 314 ha) variables that can influence adult occupancy (Hollenbeck et al., 2011; Latif et al., 2015). These included covariates related to management (percent burned and percent tree removal), habitat (canopy cover; closed [70%–100%] and open [10%–40%] canopy cover classes) and seasonal (winter and spring) climate variables (cumulative precipitation and mean temperature) at each transect survey point. We used the US Forest Service Activities Tracking System database (FACTS, https://www.fs.usda.gov/managing-land/natural-resource-manager) to determine the timing and aerial extent of forest management. We compiled canopy cover classes annually from 2012 to 2021 using the US Forest Service Tree Canopy Cover product suite (Science TCC, version 2021.4, https://data.fs.usda.gov/geodata/rastergateway/treecanopycover/) after applying a mask using LANDFIRE EVT (CONUS LF 2022, https://landfire.gov/vegetation/nvc) that maintained all tree lifeforms for existing vegetation. We used ClimateNA for summarizing climate related covariates from 2012 to 2021 (Wang et al., 2016) and calculated all landscape metrics using ArcGIS Pro 3.0 focal statistics (ESRI, 2022). We ran a model of adult occupancy with a full set of potential covariates (see Methods and Results in Supporting Information) and selected important covariates to include in the population model (Figure 2).

2.3 | Modelling framework

We aimed to understand the combined effects of climate, habitat and management variables on the three white-headed woodpecker populations. To develop this understanding and to address our research questions, we implemented a modularized modelling process. First, we fit a Bayesian statistical model to each life-stage-specific dataset available for each population: (1) egg production, (2) egg survival, (3) nestling survival, (4) dynamic adult occupancy (using the 'persistence' term as a proxy for initial population size and adult survival) and (5) pre-fledgling sex ratios. Second, we used 1050 posterior samples of the regression coefficients (covariate effects and intercepts) from each statistical model as inputs, along with original

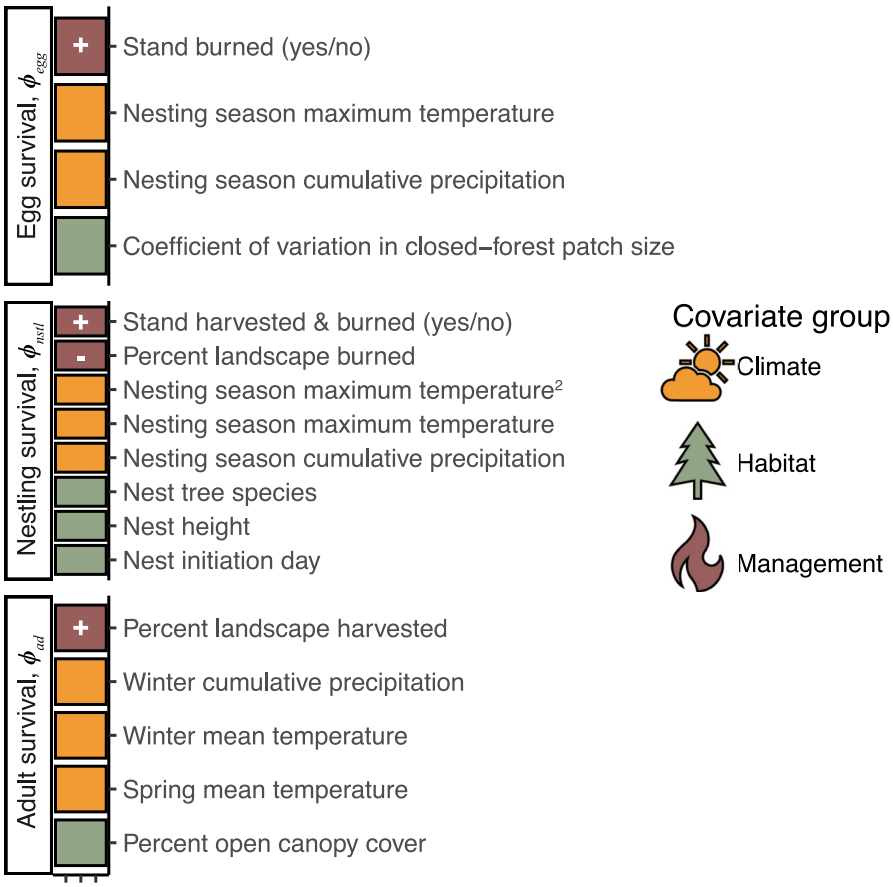


FIGURE 2 Covariates that had significant effects and that were included in final statistical models (egg survival, nestling survival and adult persistence as a proxy for survival; no important covariates for egg number or fledgling female ratios). Covariates in different covariate groups are indicated by colour: Climate (yellow/orange), habitat (green) and management (red/brown). The direction of habitat management covariate effects is indicated with '+' and '−' icons.

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nest- and landscape-scale covariates in a stage-structured population model.

An alternative approach would have been to build an integrated population model (IPM) where individual datasets (e.g. egg, nestling and adult occupancy) jointly inform data likelihoods (Schaub & Abadi, 2011). We elected to implement the two-step approach instead of fitting an IPM to all data simultaneously for various reasons that are likely common in similar monitoring datasets. First, in integrated models, larger datasets often have undue influence on model parameters, even parameters associated with other life stages (e.g. Lee et al., 2015), and so the largest dataset (adult occupancy survey points) could heavily inform covariate effects for life stages for which adult occupancy should have no ecological effect (e.g. occupancy data could shape the effect of prescribed burning on egg survival). In our case, the adult occupancy datasets are 100× larger than the nest productivity datasets (compared with relatively more similar-sized datasets integrated in many other IPM applications, Figure S1, Zipkin & Saunders, 2018). In addition to being ecologically misleading, combining three datasets with four to eight covariate effects would likely lead to computational issues in a Bayesian model (e.g. convergence and identifiability issues; Ogle & Barber, 2020). Some IPM applications set a priori weights for different datasets (Francis, 2011); however, in this case, we did not have 'high' and 'low' information value datasets on similar life stages in the same model (e.g. census counts and mark–recapture data jointly estimating population abundance and adult survival; Saunders et al., 2019). Our approach does propagate uncertainty in parameters throughout the process, however, and is equivalent to approaches such as modularization and feedback control in which joint models with dependency between joint likelihoods can be defined and controlled (Bayarri et al., 2009; Lunn et al., 2009; Molitor et al., 2009; Ogle et al., 2013). Below, we provide more details on each step in the two-step modelling process.

2.4 | Step 1: Statistical models for population life-stage data

For egg production, egg survival and nestling survival, we used covariates previously shown to be important for each life stage (Miller-ter Kuile et al., 2023). For adult survival, we used a dynamic, multi-season occupancy model including only those covariates that had non-zero effects based on Bayesian *p*-values from a model with all potential covariates (see Supporting Information; Royle & Kéry, 2007). We used covariates that drive year-to-year persistence at survey locations as covariates for both initial adult occupancy and as a proxy for adult apparent survival. We compared these survival estimates to reported values (Kozma et al., 2022) to ensure they were within reasonable ranges for white-headed woodpeckers in similar habitats (Figure S2). Covariates for all statistical models are summarized in Figure 2 and their directional effects are summarized in the Supporting Information (Figure S3). We also determined that the proportion of female near-fledging nestlings was not related to variables that could potentially impact sex ratios in birds, including brood size and nest initiation date (larger male young often do better in larger broods and in later broods; Koenig et al., 2001; Van Oosten & Schekkerman, 2021).

2.4.1 | Egg number, egg survival, nestling survival and sex-ratio models

For each life stage, we implemented a separate model for each population motivated by results from Miller-ter Kuile et al. (2023) but simplified for the purpose of this study. We developed Bayesian generalized linear models (GLMs) for each dataset, using an appropriate distribution for the likelihood and a link function appropriate to each distribution. We implemented a Poisson model with a log link for egg number, and binomial models with logit links for egg survival, nestling survival and sex-ratio data (number of female nestlings and total clutch size). The log- or logit-scale linear predictor, μ, for each model (i.e. for each life-stage and population) followed the same form such that for observation i:

$$\mu_i = \beta_{0_{f(i)}} + \sum_{j=1}^{J} \beta_j \cdot X_{j,s(i),t} + \epsilon_{s(f)} \quad (1)$$

where $f(i)$ and $s(i)$ denote the forest landscape, f ($f=1, 2, 3$), and survey or nest location, s ($s=1, 2, \ldots, N$, where N varies by landscape), associated with observation i, respectively; j indexes the covariate ($j=1, 2, \ldots, J$, where J may vary depending on dataset or life stage), and t denotes year. Each covariate, X_j, varies by nest location and year. We included additive random transect effects, ϵ_s. The random transect effects, however, are not incorporated into the population model as the population model is meant to represent the contiguous populations of white-headed woodpeckers, integrating across all observed and unobserved transects.

Thus, μ describes the expected log-scale egg number, the logit-scale probabilities of egg survival or nestling survival, or the logit-scale probability of a nestling being female. For the egg number model, however, no covariates were included, resulting in a simplified model, $\mu = \beta_{0_f}$, thus allowing expected egg number to solely vary by forest landscape ($f=1, 2, 3$). Graphical models summarizing each of these statistical models can be found in Figure S4.

2.4.2 | Adult survival: Dynamic occupancy model

As a proxy for adult survival, we developed a dynamic occupancy model for adults that estimated first-year occupancy probability, ψ, yearly values of adult persistence, ϕ_{ad}, and yearly values for colonization, γ (Royle & Kéry, 2007). This dynamic occupancy model had a standard structure for these kinds of models, including (1) an observation process model for the observed occupancy data, which is linked to the detection probability, p, and the latent occupancy, z, which is in-turn linked to (2) a biological process model that accounts for the initial occupancy probability, ψ, adult persistence probability, ϕ_{ad}, and

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colonization probability, γ. In this type of model, each of these terms (p, ψ, ϕ_{ad} and γ) can be modelled as a function of covariates that are likely to influence each process. In our model, we included a regression model for persistence probability, ϕ_{ad}, but we did not provide covariates for the detection probability, p, or the other population parameters, ψ and γ, though we allowed γ to vary from year to year. Because these models are well-developed and described elsewhere (Royle & Kéry, 2007), we have provided model equations in the Supporting Information. Also see the Supporting Information for results from an initial set of models that we implemented to assist with variable selection, which included covariates for p.

2.4.3 | Relative importance of covariate groups in statistical models

Because we wanted to know how habitat management activities differentially influence populations across habitat and climate contexts, we divided the covariate groups within our models into these three categories: (1) management, (2) climate and (3) habitat (Figure 2). While it could be argued that management activities shape habitat conditions (e.g. tree densities), we chose to split covariates in this way since management covariates describe the specific management activities enacted on the habitat (e.g. prescribed burning and tree removal), which could be considered temporary disturbances to the habitat, and habitat features primarily describe the underlying habitat conditions in which that management occurred. For each statistical model for each population, we determined the relative importance of our three types of covariates (management, climate and habitat) using hierarchical partitioning (e.g. Zylstra et al., 2021). This method uses comparisons of goodness-of-fit metrics (e.g. log-likelihood) of nested models to determine how much of the model fit is explained by different sets of covariates. We followed Zylstra et al. (2021), whereby we grouped covariates based on the above categories and averaged the differences in log-likelihoods of nested models. Specifically, we averaged the fit at each hierarchical level (number of covariate groups) then averaged across these hierarchical levels to determine the relative contribution of each covariate group to variation in the response data. We performed this hierarchical partitioning for each life stage in each population separately because we aimed to quantify how the management, climate and habitat conditions experienced by each population may differentially impact the relative importance of these drivers.

2.4.4 | Implementation of statistical models

We implemented each life stage statistical model (and the hierarchical partitioning process) separately for each population to generate population-specific covariate effects to incorporate into the population model. All models were fit using standard MCMC simulation methods. For the life stage statistical models (including the models applied to estimate covariate effects and the models applied to estimate hierarchical partitioning), we optimized each simulation by running an initial, shorter run of approximately 4000 iterations to estimate how long each model would take to converge on each parameter's posterior distribution. We then determined the necessary number of iterations and a sufficient burn-in period for each model using the Raftery diagnostic (Raftery & Lewis, 1995). We ensured that these final models converged (Gelman-Rubin diagnostic, $\hat{R}$ for every parameter <1.1, except for occupancy models, for which we set a convergence level of <1.2; Gelman & Rubin, 1992) and checked that there was no serious autocorrelation, thinning models and re-running them if necessary. Goodness-of-fit for each of the models for the nest stages was reported in Miller-ter Kuile et al. (2023). We generated similar goodness-of-fit values for the adult occupancy model (including all covariates) by generating replicated data under the mean model and comparing expected values to observed values.

2.5 | Step 2: Population model overview

To incorporate the statistical models into the population model, we built a stage-structured, female-only population model that included eggs, nestlings, fledglings, breeding adults and non-breeding adults (Figure 3). This model included rates of egg production (f) and transitions between different population stages, including egg survival (ϕ_{egg}), nestling survival (ϕ_{nstl}), fledgling survival (ϕ_{fl}) (within a year), adult survival (ϕ_{ad}) and adult transition between breeding and non-breeding states (w) (at the end of a year). Fledglings that survive (within a year) are divided into the fraction that transitions to breeding (p_{Br}) and non-breeding ($1\text{-}p_{Br}$) adults. We did not estimate inputs/losses due to immigration/emigration because we assumed populations were relatively closed within the timeframe of data collection (nesting season; May–August) and because these estimates can be biased when no data are available to inform them (Paquet et al., 2021). The population model thus simulates the numbers of eggs (N_{egg}), nestlings (N_{nstl}) and fledglings (N_{fl}) within a year and the numbers of breeding adults (N_{Br}) and non-breeding adults (N_{NBr}) at the end of a year within a CFLRP landscape.

The population model includes modules for egg production, nestling survival, fledgling survival and adult survival, all of which are informed by the life stage statistical models implemented in Step 1. Hence, the model includes important environmental covariates for each vital rate based on the statistical models. Inputs to the model included as follows: (1) relevant covariate timeseries for each nest location and a set of 'potential occupancy' points for adults (more information below in this section) and (2) 1050 posterior samples of the covariate effects and intercept values from each life stage statistical model (i.e. 350 independent samples from each of three MCMC chains). We sampled from the posterior distributions by randomly drawing a posterior sample of associated parameters (intercepts and covariate effects) from the 1050 values for each complete simulation of the population model. As a result, within a given complete run of the model, a vector of parameters was drawn from the posterior distributions generated by the statistical models, thus maintaining the posterior correlation structure of the parameters.

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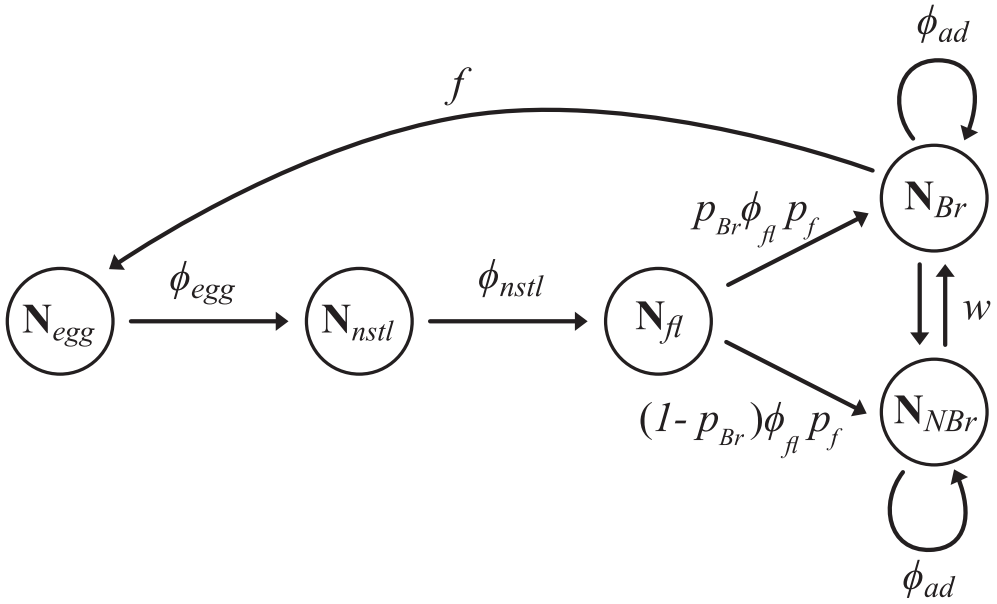


FIGURE 3 Graphical representation of the stage-structured population model for white-headed woodpeckers. Circles indicate state variables or population counts (eggs, N_{egg}; nestlings, N_{nstl}; fledglings, N_{fl}; breeding adults, N_{Br}; and non-breeding adults, N_{NBr}) and arrows represent transitions or rates (e.g. survival rates for egg survival, ϕ_{egg}; nestling survival, ϕ_{nstl}; fledgling survival, ϕ_{fl}; adult survival, ϕ_{ad}; and fecundity, f). The number of fledglings entering either adult class is dependent on the proportion of breeding adults, p_{Br} and the proportion of adults in the population that are female p_f. A small proportion, w, of individuals switch between the breeding and non-breeding states each year. This is a female-only model.

We summarized rates of transition between population stages at the yearly level by averaging across nests or potential adult occupancy locations within a year. When any of the three populations were not surveyed for a given vital rate in a given year, we estimated the missing transition probability values based on the mean of that vital rate for the year before and the year after for that population (to account for potential temporal correlation in forest management variables).

We assumed that nests were randomly sampled from the total 'population' of nests for white-headed woodpeckers associated with each forest landscape such that nests represented the range of possible conditions for each of the three populations.

Conversely, because the adult occupancy survey design oversampled areas that experienced forest management relative to the total national forest landscape, we did not assume that survey locations represented a random sample of possible occupied points. Instead, we used these data for fitting the adult occupancy life stage statistical model (see Section 2.4.2), from which we pulled the intercept and covariate effect posterior samples. We then generated a set of gridded 'potential occupancy' points for each population (Fremont–Winema: $n = 3925$; Malheur: $n = 4199$; Payette: $n = 3937$) at a regular distance of 1 km across each entire CFLRP landscape. The distance between points was based on previous studies on space use and home range size for white-headed woodpeckers (Wright, 2022). We pulled covariate values for each of the gridded points from remotely sensed datasets (including: FACTS, ClimateNA, Science TCC and LANDFIRE EVT, see Section2.2.2) to better represent the underlying distribution of important covariates for adult population rates.

2.5.1 | Initial conditions

We initialized the population model with a set of first-year population numbers and rates. We used information from nests located during first-year surveys specific to each of the three populations to set the initial conditions for nest egg number (N_{egg}), egg survival (ϕ_{egg}) and nestling survival (ϕ_{nstl}). We used the persistence probability (ϕ_{ad}) covariates from the adult occupancy statistical model to initialize year 0 adult population size (since adult numbers represent individuals present at the end of a year) at each 'potential occupancy' grid point i, along with estimating first-year occupancy probability (ψ_{1_i}). Because adult population numbers only consider females and are split between breeding and non-breeding classes, we also accounted for breeding status and sex ratios in the initial occupancy value. We first estimated point-level counts for breeding and non-breeding females using breeding (p_{BA0_i}) or non-breeding (p_{NBA0_i}) probabilities, first-year survival probability (ψ_{1_i}), and either dividing the number of birds by 0.5 (for breeding pairs) or by the posterior samples of the female sex ratio from the sex-ratio model, p_f. The probability of a breeding or non-breeding adult at a given point is given by:

$$p_{\mathrm{Br}_{0,i}} = \psi_{1_i} \cdot p_{\mathrm{Br}} \cdot 0.5 \quad (2)$$

$$p_{\mathrm{NBr}_{0,i}} = \psi_{1_i} \cdot (1 - p_{\mathrm{Br}}) \cdot p_{\mathrm{f}} \quad (3)$$

And then point-level occupancy of a breeding, Z_{Br}, or non-breeding, Z_{NBr}, female at that point is sampled from the Bernoulli distribution:

$$Z_{\mathrm{Br}_{0,i}} \sim \mathrm{Bernoulli}\left(p_{\mathrm{Br}_{0,i}}\right)$$

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$$Z_{\mathrm{NBr}_{0,i}} \sim \mathrm{Bernoulli}\left(p_{\mathrm{NBr}_{0,i}}\right) \quad (4)$$

We summed these values across points to produce initial population sizes for breeding and non-breeding adults at the end of year 0 (start of Year 1), N_{Br_0} and N_{NBr_0}, respectively.

In the first year, the number of eggs at each potential occupancy point varies stochastically around the estimated per-nest egg number in that year (f_t) from the life stage statistical model. Whether there are eggs is conditioned on there being a breeding adult at that potential occupancy point. Thus, eggs for the first year:

$$\mathrm{egg}_i \sim \mathrm{Poisson}\left(f_0 \cdot Z_{\mathrm{Br}_{0,i}}\right) \quad (5)$$

Like the adult values, the total number of eggs in the first year, N_{egg}, is the sum of the nest-level eggs across all potential occupancy points *i*.

2.5.2 | Yearly simulations of vital rates and population sizes

In subsequent years, the approach to calculating egg number (per adult, *f*), egg survival (ϕ_{egg}), nestling survival (ϕ_{nstl}), fledgling survival (ϕ_{fl}) and adult survival (ϕ_{ad}), remained the same, all indexed by year *t*. In all years, these values feed into total population sizes for each stage (Figure 3). These equations for all nest stages are:

$$N_{\mathrm{egg}_t} = f_t \cdot N_{\mathrm{Br}_{t-1}}$$

$$N_{\mathrm{nstl}_t} = \phi_{\mathrm{egg}_t} \cdot N_{\mathrm{egg}_t}$$

$$N_{\mathrm{fl}_t} = \phi_{\mathrm{nstl}_t} \cdot N_{\mathrm{nstl}_t} \quad (6)$$

For years following the first year, adult populations (breeding, N_{Br_t}, and non-breeding, N_{NBr_t}) were dependent on (1) *recruitment*: the number of female fledglings entering the adult population in each breeding class based on the number of fledglings that survive, the proportion of breeding versus non-breeding adults and the sex-ratio (proportion female, p_f), (2) *survival*: number of adults last year that survived to current year, based on their survival probability, ϕ_{ad}, and (3) *adult transitions*: number of adults that transition between the breeding and non-breeding states based on the transition probability, *w*. Thus, yearly breeding and non-breeding female populations are given as:

$$N_{\mathrm{Br}_t} = \phi_{\mathrm{fl}} \cdot N_{\mathrm{fl}_t} \cdot p_{\mathrm{Br}} \cdot p_f + N_{\mathrm{Br}_{t-1}} \cdot \phi_{\mathrm{ad}_t} + N_{\mathrm{Br}_{t-1}} \cdot \phi_{\mathrm{ad}} \cdot w - N_{\mathrm{Br}_{t-1}} \cdot \phi_{\mathrm{ad}} \cdot w$$

$$N_{\mathrm{NBr}_t} = \phi_{\mathrm{fl}} \cdot N_{\mathrm{fl}_t} \cdot (1 - p_{\mathrm{Br}}) \cdot p_f + N_{\mathrm{NBr}_{t-1}} \cdot \phi_{\mathrm{ad}_t} + N_{\mathrm{Br}_{t-1}} \cdot \phi_{\mathrm{ad}} \cdot w - N_{\mathrm{NBr}_{t-1}} \cdot \phi_{\mathrm{ad}} \cdot w \quad (7)$$

For all years, we determined the probability of breeding, p_{Br}, by determining the mean and variance of the proportion of adults detected during point surveys that were also in proximity of a known nest. We then sampled values of p_{Br} from a Beta(1.44, 1.04), whereby the arguments to the distribution satisfy $E(p_{\mathrm{Br}}) = 0.58$ and $\mathrm{Var}(p_{\mathrm{Br}}) = 0.07$, and were based on the observed mean and variance in breeding proportions from the survey data. We sampled fledgling survival, ϕ_{fl}, from a Beta(9.49, 1.54) to give values for $E(\phi_{\mathrm{fl}}) = 0.98$ and $\mathrm{Var}(\phi_{\mathrm{fl}}) = 0.01$ based on previous studies (Kozma et al., 2022). Finally, we assumed that the rate of adults transitioning between breeding and non-breeding classes in a given year, *w*, was relatively small (Kozma et al., 2022), and we thus sampled *w* from a Uniform(0,0.1) distribution. Breeding proportions, fledgling survival probabilities and breeding/non-breeding transition probabilities remained the same across years within one simulation of the population model but varied across simulations.

2.5.3 | Relative importance of covariate groups in the population model

In addition to quantifying the relative importance of different covariate groups to stage-specific rates in the life stage statistical models, we also determined how covariate groups shaped population trajectories. To do this, we performed a similar approach to hierarchical partitioning of the population model as we did for the statistical models. Because we did not have a log-likelihood for the model, we instead used differences ('sensitivities') between population growth estimates, λ, from the full model (considered 'true' population growth) and a set of nested models with combinations of covariate groups (Williams et al., 2002). Again, the covariate groups we considered included (1) climate, (2) habitat and (3) management.

To derive λ, we first determined the total yearly adult population size, N_t, for each simulation of the population model for each of the three populations by adding the number of breeding and non-breeding adults in each year *t* as follows:

$$N_t = N_{\mathrm{Br}_t} + N_{\mathrm{NBr}_t} \quad (8)$$

Then, we calculated discrete-time population growth rate, λ, by estimating λ for each model simulation as the finite rate of increase between one time point (year) and the next (Saunders et al., 2019):

$$\lambda_{t+1} = \frac{N_{t+1}}{N_t} \quad (9)$$

2.5.4 | Running the population model

We ran the population model for each of the three populations and also ran the hierarchical partitioning process for the population using population and life stage statistical model-specific covariate values (e.g. the effect of cumulative precipitation in the hierarchical partitioning process for the population model depended on population location and other covariates included in that specific statistical model). We ran the full population model for 1000 simulations for each population and calculated summary statistics for vital rates. We ran the sensitivity analyses for 1000 simulations as well, using mean values for λ from each nested model to determine sensitivity to covariate groups.

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2.6 | Modelling software and reproducibility

We ran all code in R (version 4.2.2; R Core Team, 2020) and used JAGS (version 4.3.1; Plummer, 2003). All data and code to generate all data cleaning, analyses and figures for this paper can be found on Zenodo (https://doi.org/10.5281/zenodo.15843963; Miller-ter Kuile et al., 2026). More information on all modelling steps, implementation and reproducibility can be found in the Supporting Information.

3 | RESULTS

3.1 | Importance of environmental drivers for life stages

The following paragraphs summarize the life stage panels (a–c, e–g and i–k) in Figure 4, which illustrates hierarchical partitioning results. For egg survival, habitat management variables were more important than habitat and climate variables for the Malheur population (40% relative importance, versus 34% and 26% for climate and habitat, respectively). For the other two populations, climate variables were of much greater importance than either management or habitat variables (80% and 74% relative importance for climate variables for the Fremont–Winema and Payette populations, respectively). Of the three populations, the Malheur population also had the strongest habitat effect (34% vs. 10% and 8% for the Fremont–Winema and Payette populations, respectively). Management confers a benefit to egg survival for white-headed woodpeckers—in locations where the stand surrounding a nest tree received prescribed burning treatments, more eggs survive (Miller-ter Kuile et al., 2023).

For nestling survival, management variables were the most important variables for the Fremont–Winema population (51% relative importance, versus 40% and 9% for climate and habitat, respectively). Again, climate variables were the most important for the other two populations (67% and 68% relative importance for the Malheur and Payette populations, respectively). Habitat variables had the greatest influence in the Payette population (22% vs. 9% and 2% for the Fremont–Winema and Malheur populations, respectively). For nestling survival, survival is higher in areas where the immediate nest tree area has received prescribed burning and

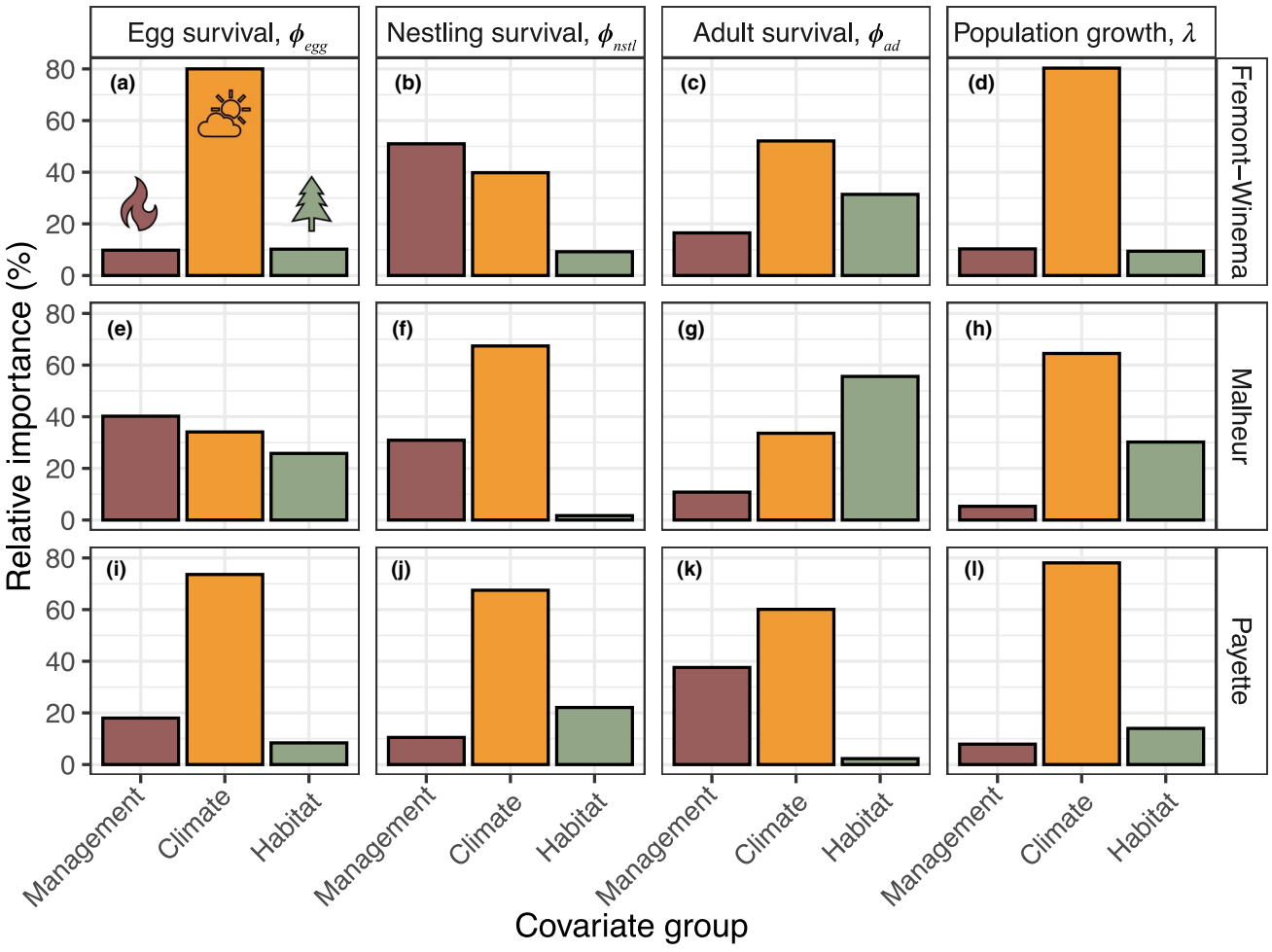


FIGURE 4 Relative importance of different covariate groups (climate, habitat and management) on life stage survival and population growth for the Fremont–Winema (a–d), Malheur (e–h) and Payette (i–l) populations of white-headed woodpeckers. Hierarchical partitioning results are summarized for egg survival (a, e and i), nestling survival (b, f and j), adult survival (c, g and k) and population growth (d, h and l).

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tree thinning treatments. However, as the percent of the landscape surrounding the nest (1 km radius) that received a prescribed burning treatment increases, nestling survival decreases (Miller-ter Kuile et al., 2023).

For adult survival, management variables were less important than habitat, climate or both types of variables for all populations. However, management variables were most important for the Payette population (38% relative importance, compared with 17% and 10% for the Fremont–Winema and Malheur populations, respectively). Climate variables were the most important for the Fremont–Winema (52%) and Payette (60%) populations. However, the Malheur population was most influenced by habitat variables (56%). The Fremont–Winema population was also clearly influenced by habitat variables (31%). For adult survival, management effects are positive: as the percent of the landscape (1 km radius) around occupancy survey locations increases, apparent survival also increases (Figure S5).

To summarize management importance across life stages and populations, habitat management (1) most strongly impacted nestling survival across populations (11%–51% relative importance); (2) was most influential for nestling survival in the Fremont–Winema and for egg survival in the Malheur population and was never the most influential for adult survival; (3) had a significant contribution (>25%) for egg survival in the Malheur population, nestling survival in the Fremont–Winema and Malheur populations, and adult survival in the Payette population (44% of life stage-population combinations).

3.2 | Importance of environmental drivers for the population

For overall population growth, management variables were never the most important and were insignificant relative to the overwhelming effect of climate variables (climate importance: Fremont–Winema: 80%; Malheur: 65%; Payette: 78%). Management variables were the least important for all populations but were of comparatively higher importance for the Fremont–Winema (10%) and Payette (8%) populations than for the Malheur (5.3%) population. Though habitat variables were secondary to climate variables, habitat variables were comparatively more important for the Malheur population (30%) and relatively less important for the Fremont–Winema (9%) and Payette (14%) populations.

Additional results, including model diagnostics and convergence statistics, and population trends and relationships to life stages can be found in the Supporting Information.

4 | DISCUSSION

In this study, we demonstrated how local habitat and climate conditions shaped responses of three populations of white-headed woodpeckers (*Dryobates albolarvatus*) to habitat management. Habitat management influenced egg, nestling and adult survival differently across all populations but had the greatest influence on nestling survival (11%–51% relative importance). Management actions were unimportant for population growth for all populations (5%–10% relative importance). Climate was the most important driver of population growth; however, the population with habitat conditions most like historical baselines based on forest structure and composition (Malheur, Figure 1a) was most shaped by habitat conditions. This finding suggests that as habitat management reintroduces historical conditions, habitat conditions which can be maintained via ongoing management actions will be key to population persistence for white-headed woodpeckers. Our findings are likely not unique to white-headed woodpeckers: populations experience human alterations to their habitats differently depending on their local context (Coates et al., 2018; Mantyka-pringle et al., 2012). This study builds a general population modelling approach that can be applied as a conservation planning tool in this system or that could be adapted to other species in other systems.

White-headed woodpeckers occur across a range of habitat conditions within their endemic range along the west coast of North America and our results demonstrate how this variation shapes habitat management responses (Garrett et al., 1996; Figure 1). This is key for informing future habitat management for this bird species. For one, management most influenced populations and life stages experiencing habitat conditions closer to their historical range (Malheur, Figure 1a), suggesting that as future habitat management shifts more areas towards these conditions, management will more strongly shape white-headed woodpecker populations. This is a key insight given that habitat management is an attainable local action that may be able to buffer population declines given ongoing climate change (Greenwood et al., 2016). This is in direct contrast with the Payette population, which exists in habitat conditions least like historical conditions and for which climate is the most important driver across all life stages (Figures 1a and 4). This location is also the coolest and wettest with the greatest seasonal fluctuations in temperature during the nesting season. Wetter, more variable climate conditions during the nesting season may decrease adult foraging activity and increase thermal stress of nestlings (Davis et al., 2019; Kehoe, 2017; Purcell & McGregor, 2021). In this population, ongoing and future management may shift the relative importance of climate, thus reducing climate vulnerability.

Population models that integrate multiple data sources and covariates are powerful tools for identifying life stages that serve as sinks to population persistence (Weegman et al., 2016; Zylstra et al., 2021). This may be particularly true in cases where habitat conditions that have a neutral or beneficial effect on one life stage have a negative effect on other life stages (Stillman et al., 2019). There is evidence of this pattern in the Fremont–Winema white-headed woodpecker population. This species prefers to nest in the open but near areas with denser forest habitat nearby for foraging (Garrett et al., 1996; Hollenbeck et al., 2011). However, the relative lack of conifer forest heterogeneity in the Fremont–Winema landscape may put nestling woodpeckers at risk, especially in conjunction with prescribed burning. In these forest conditions, nests are often in adjacent forest types (e.g. aspen) or may be in more exposed

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nest trees at habitat edges, both locations where predators are more common (Andrén, 1995; Hagar et al., 2024). Concurrently, in more burned landscapes, adults may need to forage farther from nests for insect resources, putting nestlings at greater risk of predation (Burger et al., 2012; Lorenz et al., 2020; Miller-ter Kuile et al., 2023; Stillman et al., 2022). Compared with the other two populations, Fremont–Winema habitats are drier during the nestling stage, which may exacerbate or interact with burning effects—as a baseline, adults may forage farther from nests to find insect food resources (Hallmann et al., 2017; Welti et al., 2022).

Though climate had variable importance across life stages and populations, climate was the most important factor for population growth for all three populations (Figure 4). Across species and continents, climate is a consistent driver of population responses, likely due to physiological regulation and because of links between climate and species interactions (Cahill et al., 2013; Pörtner & Farrell, 2008; Stephens et al., 2016). However, at the population level, we observed that habitat features can have a significant effect on populations that occur in historical conditions (Malheur; Figure 4). These results build on evidence from populations of diverse taxa across the globe that demonstrate that the combination of both local-scale habitat and broad-scale climate are important for shaping population responses (Mantyka-pringle et al., 2012; Shew et al., 2019; Williams et al., 2022).

In this study, we demonstrated how to integrate multiple available data sources, including important covariates, into modular population models that provide an alternative to the growing popularity of IPMs (Zipkin & Saunders, 2018). We demonstrated that you can use this approach using datasets with widely different sizes without over-weighting the largest datasets or giving these datasets influence over model parameters over which they have no biological control (e.g. covariate effects for other life stages; Figure S1). Many population models, integrated and otherwise, leverage data that explicitly track adult survival through mark–recapture methods (Sanderlin et al., 2019; Zipkin & Saunders, 2018). In this case, we demonstrated that our estimates from dynamic occupancy models ('persistence') aligned with the range of published adult survival estimates from similar ecosystems (Kozma et al., 2022). For other studies that lack mark–recapture data but similar species biology (e.g. territoriality) and have occupancy-type data (which is often more readily available and more economical to collect), our results suggest that occupancy data can be sufficient for estimating adult survival.

4.1 | Management implications

Our modelling approach highlights where and when management is most likely to impact populations, providing managers with insights on the timing and extent of management activities (e.g. management may have a greater impact in more open initial forest conditions and/or in locations with more moderate climate). Furthermore, while we looked at retroactive population responses, this modelling approach can accommodate simulations of future scenarios of climate, habitat and management. The modular population model can be adapted to other species and contexts in which covariate effects are important to life stage survival and for systems where datasets of unequal sizes have similar information richness for population parameters (Francis, 2011; Lee et al., 2015).

5 | CONCLUSIONS

Changes to climate and habitat are leading to biodiversity change and loss at an ever-accelerating rate (Ceballos et al., 2017; Pimm et al., 2014). This study adds to growing evidence that population regulation is linked to compounding climate and habitat factors that shape the full life history of individuals (Zipkin & Saunders, 2018). Furthermore, our study shows that populations are regulated by local environmental conditions that shape how species are likely to respond to conservation and management initiatives aimed at population persistence (Riddell et al., 2019). Building this evidence allows us to build predictive models of how populations, communities and ecosystems are likely to change in the future with and without conservation and management interventions (Lisovski et al., 2024; Schuurman et al., 2022).

AUTHOR CONTRIBUTIONS

All authors developed project questions collectively. VS designed the study. JD led collection of field data and management of data. AM-tK, KO and JSS developed the modelling approach. AM-tK led analyses, writing and visualization. All authors contributed to editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code are available on Zenodo: https://doi.org/10.5281/zenodo.15843963 (Miller-ter Kuile et al., 2026).

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STATEMENT ON INCLUSION

Several of the authors reside in the region of the study and we consulted local management practitioners in developing the study.

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SUPPORTING INFORMATION

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Figure S1. Relative dataset sizes for a set of published studies from a review (Zipkin & Saunders, 2018) that reported sample sizes ($n = 16$) and for this study. We divided the size of the smallest dataset in each study by the largest dataset to highlight the larger difference in this study but also to highlight that many studies have disproportionate dataset sizes that need to be considered for integrated methods (e.g. integrated population models).

Figure S2. Comparison of adult survival from our dynamic occupancy model overlayed with the range of published (orange horizontal region) mark–recapture survival estimates for white-headed woodpeckers (Kozma et al., 2022). Each box represents the distribution of values for each population (median and interquartile range) and the points represent yearly adult survival values for each population. The blue dashed line depicts the mean adult survival value from this study.

Figure S3. Directional effects of covariates in each statistical submodel that had important covariate effects (excludes egg number and fledgling female ratio due to a lack of important covariates).

Figure S4. General graphical models summarizing the statistical models applied to each life stage, including egg production (a), egg survival, nestling survival and proportion female nestlings (b), and

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the dynamic occupancy model (c) for estimating adult occupancy and apparent survival. Explanations of these models can be found in the main text (a and b: Equation 1; c: Equations 2–5).

Figure S5. Covariate effects for the dynamic occupancy model that was implemented to select important variables for adult persistence (a proxy for survival). Variables with significant effects based on Bayesian *p*-values are coloured in blue. Variables include mean temperature in winter and spring (Tmean_wt and Tmean_sp), winter and spring precipitation (cumulative; PPT_wt and PPT_sp), the percent of the landscape (1 km radius around survey point) burned (LandBu) and harvested (LandHa), The percent of the landscape in two canopy cover classes: open (10–40%; LowCC) and closed (70%–100%; HighCC).

Figure S6. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects and gamma) in the adult dynamic occupancy model with all covariates included.

Figure S7. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept) in the egg number model.

Figure S8. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified egg survival model.

Figure S9. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified egg survival model for the three forests.

Figure S10. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified egg survival model for the three forests.

Figure S11. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified nestling survival model for the three forests.

Figure S12. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified nestling survival model for the three forests.

Figure S13. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified nestling survival model for the three forests.

Figure S14. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the simplified adult occupancy model for the three forests. Results are synthesized across forests, though the model was run for each forest individually.

Figure S15. Summary of convergence statistics (i.e. potential scale reduction factor, $\hat{r}$) for all root nodes (e.g. intercept, covariate effects) in the sex-ratio model with all potential covariates for the three forests. All nodes converged for the simplified model as well.

Figure S16. Goodness-of-fit for the adult dynamic occupancy model with all covariates included. Goodness-of-fit is based on the area under the curve (AUC) statistic, which is a measure of how well the model distinguishes differences between observed 0 and 1 data. The distribution represents the AUC for each of 350 posterior samples and the dashed line indicates the mean AUC across posterior samples.

Figure S17. Distribution of covariate values for the egg survival model for each forest population. These include (a) the number of nests in different stand treatment categories, (b) the coefficient of variation in closed-forest (70%–100% canopy cover) patch size in the landscapes (1 km radius) around nests for each of the three populations, (c) maximum temperatures during the period of nesting when eggs were in the nest and (d) the cumulative precipitation during the egg incubation period for each of the three populations.

Figure S18. Distribution of covariate values for the adult survival model for each forest population. These include (a) the percent of landscapes around each survey point with harvested treatments, (b) The percent of the landscape around a survey point with open canopy class, (c) cumulative precipitation in the winter for each population, (d) average spring temperature for each population and (e) winter average temperatures for each population.

Figure S19. Distribution of covariate values for the nestling survival model for each forest population. These include (a) the number of nests in different stand treatment categories, (b) the percent of the landscape (1 km radius) around each nest with burned treatments, (c) nest height, (d) nest initiation date, (e) maximum temperature during the time nestlings were in nests and (f) cumulative precipitation during the period in which nestlings were in the nest for each population.

Figure S20. Relationships between population growth, λ, and stage-level survival probabilities for the Fremont–Winema (a–d), Malheur (e–h) and Payette (i–l) populations of white-headed woodpeckers. Figures include the relationships between λ and egg survival (a, e and i), nestling survival (b, f and j), adult survival (c, g and k) and the distribution of 1000 R^2 statistics for each relationship (d, h, l). In panels d, h and l, the dashed vertical lines of different colours represent the mean R^2 for each relationship. In all panels, the darkest blue represents egg survival, the medium blue represents nestling survival and the lightest blue colour represents adult survival.

Figure S21. Yearly (a, c and e) and overall (b, d and f) population trends of white-headed woodpeckers in the three populations (a and b: Fremont–Winema; c and d: Malheur; e and f: Payette). Dashed horizontal lines at $\lambda = 1$ in all panels indicate stable population growth. Values above this line indicate populations are increasing; below this line populations are declining. Point values are mean population growth and error bars represent one standard deviation. Mauve coloured boxes indicate years in which active restoration-based forest management occurred for each population.

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