THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 121, 2019, pp. 1–13
DOI: 10.1093/condor/duz004

RESEARCH ARTICLE

No evidence of a demographic response to experimental herbicide treatments by the White-crowned Sparrow, an early successional forest songbird

James W. Rivers,[1,*] Jake Verschuyl,[2] Carl J. Schwarz,[3] Andrew J. Kroll,[4] and Matthew G. Betts[1,5]

[1] Department of Forest Ecosystems & Society, Oregon State University, Corvallis, Oregon, USA
[2] National Council for Air and Stream Improvement, Anacortes, Washington, USA
[3] Department of Statistics and Actuarial Science, Simon Fraser University, Burnaby, British Columbia, Canada
[4] Weyerhaeuser, Federal Way, Washington, USA
[5] Forest Biodiversity Network, Department of Forest Ecosystems & Society, Oregon State University, Corvallis, Oregon, USA
* Corresponding author: jim.rivers@oregonstate.edu

Submission Date: July 9, 2018; Editorial Acceptance Date: December 28, 2018; Published April 4, 2019

ABSTRACT

Early-successional forest birds, which depend on disturbance events within forested landscapes, have received increased conservation concern because of long-term population declines. Herbicides are often used to control vegetation within early-successional forests, with unknown effects on avian vital rates. We used a large-scale experiment to test how nest and post-fledging survival were influenced by herbicide intensity within managed conifer plantations across 2 breeding seasons. We created a gradient of 4 stand-scale herbicide treatments (light, moderate, and intensive, and no-spray control) and evaluated the reproductive response of the White-crowned Sparrow (*Zonotrichia leucophrys*), a declining songbird in managed forest landscapes of the Pacific Northwest. Against initial predictions, we found no evidence that either daily nest survival (n > 760 nests across all treatments) or post-fledging survival (n = 70 individuals reared in control and moderate treatments) were influenced by herbicide application intensity. Increased herbicide intensity resulted in an extensive reduction in vegetation cover at both stand and nest-patch scales; in contrast, vegetative cover at nest sites did not differ across herbicide treatments, nor was nest survival related to vegetation concealment measures. As the largest experimental investigation to assess forest herbicide effects on songbird demography, our study indicates that components of sparrow reproductive success were not influenced by experimental vegetation control measures, although additional work on other early-successional species will be useful to evaluate the generalities of our findings.

Keywords: early-successional forest, forest herbicides, intensive forest management, nest survival, post-fledging survival, reproductive success

Falta de evidencia de una respuesta demográfica a tratamientos experimentales con herbicidas por parte de *Zonotrichia leucophrys*, un ave canora de la sucesión forestal temprana

RESUMEN

Las aves de la sucesión forestal temprana, que dependen de eventos de disturbio dentro de los paisajes boscosos, son una preocupación creciente de conservación debido a las disminuciones poblacionales de largo plazo. Los herbicidas se emplean usualmente para controlar la vegetación en los bosques sucesionales tempranos, aunque falta una comprensión profunda sobre cómo la aplicación intensiva de herbicidas influencia las tasas vitales de las aves que determinan el reclutamiento poblacional. Usamos un experimento de gran escala para evaluar cómo la supervivencia del nido y la supervivencia post emplumamiento estuvieron influenciadas por la intensidad del herbicida dentro de plantaciones de coníferas manejadas a lo largo de dos estaciones reproductivas. Creamos un gradiente de cuatro tratamientos con herbicida a la escala de rodal (suave, moderado, intensivo y control sin aspersión) y evaluamos la respuesta reproductiva de *Zonotrichia leucophrys*, un ave canora en disminución en paisajes boscosas manejados del noroeste del Pacífico. En contra de nuestras predicciones iniciales, no encontramos evidencia de que la supervivencia diaria del nido (n > 760 nidos a lo largo de todos los tratamientos) ni la supervivencia post-emplumamiento (n = 70 individuos criados en tratamientos control y moderado) estuvieron influenciadas por la intensidad de la aplicación del herbicida. Un aumento en la intensidad del herbicida produjo una reducción extensiva en la cobertura de la vegetación tanto a escala de rodal como de parche del nido; en contraste, la cobertura de la vegetación en los sitios del nido no varió a través de los tratamientos de herbicida, ni la supervivencia del nido estuvo relacionada con las medidas de supresión de la vegetación. Nuestro estudio, que representa la mayor investigación experimental para evaluar los efectos de los herbicidas forestales en la demografía de las aves canoras, revela que los componentes del éxito reproductivo de *Zonotrichia leucophrys* no

estuvieron influenciados por las medidas experimentales de control de la vegetación, aunque sería útil contar con trabajos adicionales sobre otras especies de la sucesión temprana para evaluar las generalidades de nuestros hallazgos.

Palabras clave: bosque sucesional temprano, éxito reproductivo, herbicidas forestales, manejo intensivo del bosque, supervivencia del nido, supervivencia post-emplumamiento

INTRODUCTION

The increased global demand for timber (FAO 2016) has led to an intensification of forest management practices undertaken to maximize wood production, especially within industrial forest plantations (Carle and Holmgren 2008, Rodriguez et al. 2014). Intensive forest management practices in forest plantations vary but often include shortening rotation age, planting monocultures of genetically improved tree seedlings, undertaking site preparation prior to planting, and using herbicides to control competing vegetation (Guynn et al. 2004, Adams et al. 2005, Wagner et al. 2006). Of these, the use of herbicides is arguably the most widespread management tool used during the initial period after timber harvest (i.e. <5 yr; Shepard et al. 2004, Wagner et al. 2006) and it remains one of the most controversial (Freedman 1991, Wagner et al. 1998, Shepard et al. 2004, Flueck and Smith-Flueck 2006). Herbicides make use of chemical actions to suppress competing vegetation and promote the growth of crop trees (Shepard et al. 2004, Wagner et al. 2004, Newton 2006), and their use can lead to substantial increases in timber yield (Wagner et al. 2004, 2006). Within especially productive regions of the world, such as the Pacific Northwest region of the United States (Talbert and Marshall 2005), controlling competing vegetation with herbicides is thought to be the only economically viable approach that allows landowners to avoid punitive actions from legally mandated reforestation standards during the period immediately after harvest (Rose and Coate 2000, Wagner et al. 2004). Nevertheless, herbicide use simplifies plant communities within developing forests (Shepard et al. 2004) and often truncates the period that early-successional forests are available (Franklin et al. 1986, Swanson et al. 2011), both of which are thought to reduce the conservation value of these habitats (Franklin et al. 1986, MacKinnon and Freedman 1993, Easton and Martin 1998).

Despite their widespread use (Shepard et al. 2004), surprisingly little is known about the influence of forest herbicides on the vital rates that structure animal populations, including birds within intensively managed landscapes (Lautenschlager and Sullivan 2004, Hayes et al. 2005, Stephens and Wagner 2007, Brockerhoff et al. 2008). Indeed, previous studies have been restricted largely to evaluating how bird species richness and breeding density are linked to herbicide use in early-successional forest (e.g., Morrison and Meslow 1984, MacKinnon and Freedman 1993, Lautenschlager and Sullivan 2004), with only a single study examining the link between herbicide use and avian vital rates (Easton and Martin 1998, 2002). That study quantified nest survival within older conifer forests (i.e. 11–22 yr post-harvest) whose structure and composition differ markedly from forests in the initial period of forest succession. Therefore, it remains unclear how herbicides impact avian vital rates, including post-fledging survival, of bird species that require early-successional forest and are sensitive to short-term changes in vegetation immediately after harvest (Betts et al. 2013, Perry and Thill 2013, King and Schlossberg 2014). Investigations that evaluate both components of reproductive success (i.e. nest survival and post-fledging survival) along a continuum of herbicide application intensity are needed to understand how these practices influence recruitment in forest bird populations, including how songbird productivity can be balanced with wood production (Betts et al. 2013).

In this study, we used a large-scale manipulative experiment to test the hypothesis that forest herbicide application intensity (hereafter, herbicide intensity) negatively influences vital rates of an early-successional bird species that breeds in regenerating conifer forests. We measured nest survival and post-fledging survival of the White-crowned Sparrow (*Zonotrichia leucophrys*) along a continuum of herbicide intensity on recently harvested Douglas-fir (*Pseudotsuga menziesii*) stands. Because forest herbicides target plant physiological mechanisms and are not known to have direct effects on forest animal populations at prescribed levels (Tatum 2004, McComb et al. 2008), we focused our study on evaluating the indirect effects of herbicides on bird vital rates. We predicted that both nest and post-fledging survival would be inversely related to herbicide intensity given that herbicides decrease vegetation cover, and that such reduction would be expected to provide less concealment for nests and dependent young and ultimately reduce survival rates (Martin and Roper 1988, Martin 1992, Vitz and Rodewald 2011). It is well known that 2 time-dependent covariates, nest age and nest initiation date, can have important consequences for nest survival (Grant et al. 2005), so we also evaluated the degree to which herbicide intensity was linked to these time-based measures.

METHODS

Study Area and Focal Species

We conducted our study in the Coast Range of western Oregon, USA, during the 2013 and 2014 breeding seasons (May–Aug). This area is a coastal temperate rainforest and receives 250–300 cm of precipitation annually, primarily

as winter rain. Land ownership consists of private industrial, private non-industrial, state (Oregon Department of Forestry), and federal (U.S. Forest Service, Bureau of Land Management) lands. Our study region is classified as the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988) although the majority of stands in our study area are second-growth Douglas-fir, with lesser amounts of grand fir (*Abies grandis*) and western redcedar (*Thuja plicata*). Early-successional forests in this region contain a diversity of grasses, ferns (especially bracken fern [*Pteridium aquilinum*] and western sword fern [*Polystichum munitum*]), evergreen ground cover (e.g., salal [*Gaultheria shallon*], Oregon grape [*Mahonia nervosa*]), and broadleaf shrubs (e.g., vine maple [*Acer rubra*], bigleaf maple [*Acer macrophyllum*], red elderberry [*Sambucus racemosa*], *Rubus* spp.), many of which compete with commercial trees within plantations.

Our study was designed to assess how songbird nest survival and post-fledging survival were influenced by a range of herbicide intensities, with a focus on declining songbird species that use non-commercial vegetation as nesting and foraging substrates within early-successional forests. Of several candidate bird species identified by initial surveys (Betts et al. 2013), the White-crowned Sparrow (hereafter sparrow) was the only species that fulfilled all of our requirements. This species is restricted to early-successional conditions within forests of the Pacific Northwest (Chambers et al. 1999), and pilot data indicated that sparrows nested on stands representing all herbicide treatments prior to the start of our study (Betts et al. 2013). Importantly, this allowed us to evaluate their demographic response across the entire continuum of herbicide intensity, which was not the case for other declining songbirds in our system. In addition, the sparrow has experienced a long-term population decline in Oregon, with data from the Breeding Bird Survey indicating a decrease of 3.62% per year (95% CI: 2.94, 4.37) from 1966 to 2013 (Sauer et al. 2014). Sparrows target invertebrates for food during the breeding season, including lepidopteran larvae (Chilton et al. 1995) that are largely restricted to non-coniferous vegetation within intensively managed forests (Hammond and Miller 1998, Wagner et al. 2004, Hagar et al. 2007). Finally, our previous experience with sparrows indicated that reproductive data could be obtained with relative ease within early-successional forest, as sparrows typically build their nests close to the ground in microhabitats easily accessed by researchers and exhibit behaviors within the vicinity of nests that facilitate nest location (Rivers et al. 2011).

Experimental Design and Herbicide Treatments

Our study was part of a larger investigation whose aim was to evaluate the potential tradeoffs between biodiversity and timber production in intensively managed Douglas-fir plantations. The overall experimental design consisted of a randomized complete block design that comprised 8 study blocks on stands along a ~100 km north–south gradient (Betts et al. 2013). We established 4 stands within each study block and we randomly assigned 1 of 4 treatments to each stand, with treatments applied at the stand scale for a total of n = 32 stands. For this study, we selected a subset of 4 blocks (n = 16 stands, 4 replicates per treatment) to evaluate in both years of study to maximize per-stand field effort, as our goal was to locate as many nests as possible on each stand. All stands within each study block were situated within 5 km of each other to provide spatial independence while limiting extraneous variation due to heterogeneity at the landscape scale. Stand size was typical for forest harvest operations in our region (12–16 ha), and all stands underwent harvest in fall 2009/winter 2010 and were replanted in 2011 with bare-root Douglas-fir seedling nursery stock.

We used an experimental design in which each of 4 stands within each block was subjected to 1 of 4 distinct treatments that were applied to the entire stand: light, moderate, and intensive herbicide application, and no-spray control (Figure 1, Supplemental Material Appendix A). Briefly, stands in the no-spray control group received no herbicide application before or after harvest. Stands in the light herbicide treatment were treated with a spring herbaceous release spray in the first post-harvest year (2011) and a broadleaf release spray in the second post-harvest year (2012) and as needed in 2014. In the moderate herbicide treatment, which served as a proxy for contemporary operational practices, stands received a site preparation herbicide application prior to planting, followed by a spring herbaceous release spray in the first post-harvest year (2011). In the intensive herbicide treatment, stands received a site preparation herbicide applied prior to planting followed by aerial spring herbaceous release sprays in years 1–3 post-harvest (2011–2013) and an aerial broadleaf release spray in the second post-harvest year (2012). Follow-up backpack spraying to control deciduous stump sprouts was conducted on the intensive treatment as needed to standardize treatments across stands. For all stands that received herbicides via aerial spraying, application occurred prior to the beginning of the local sparrow breeding season (1 May) in all years herbicides were applied. Our herbicide treatments led to substantial reductions in broadleaf cover and species richness of broadleaf plants across the experimental gradient (Betts et al. 2013, Kroll et al. 2017), including during the period when we measured sparrow demographic response in years 3 and 4 post-harvest (see Results).

Quantification of Nest Survival and Post-fledging Survival

We searched for sparrow nests during the local breeding seasons (May–Jul) using a combination of systematic searches and focused behavioral observations such that similar nest-searching effort was undertaken on each stand in each year. Once located, we monitored each nest

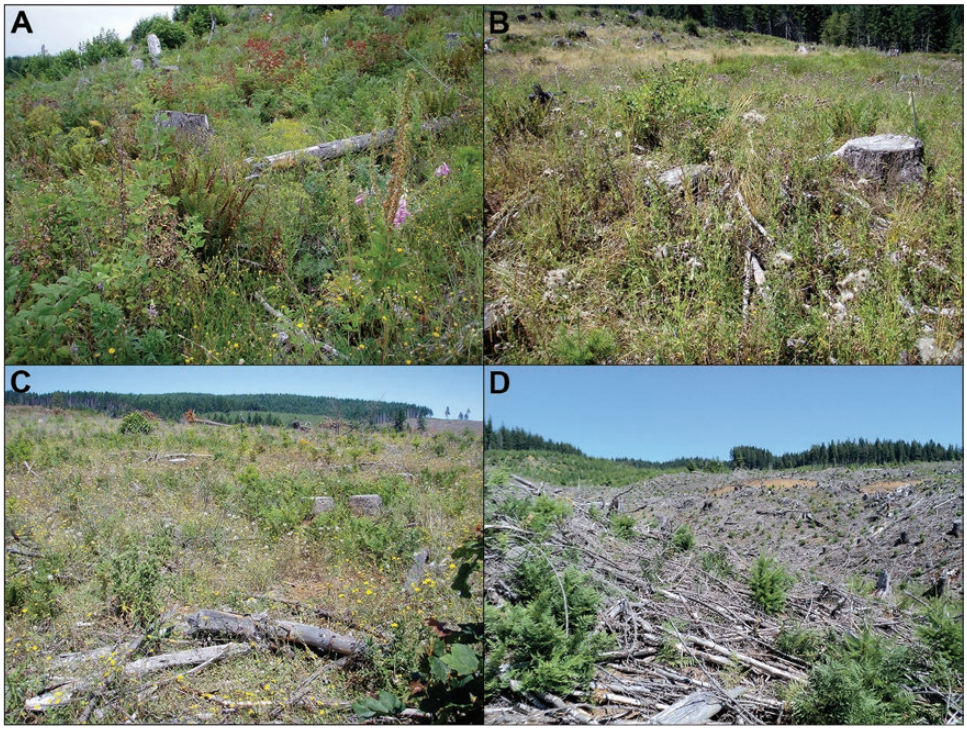

FIGURE 1. Representative images of the 4 experimental herbicide treatments used in this study consisting of (**A**) no-spray control, (**B**) light herbicide application, (**C**) moderate herbicide application, and (**D**) intensive herbicide application. All photos were taken during July 2013. Photos A–C: Thomas Stokely, Photo D: Jake Verschuyl.

every 2–3 days to determine its fate; we deemed a nest successful if its end date was consistent with the expected fledging date and there was evidence of fledglings nearby through visual confirmation of parental behavioral responses. Sparrows can produce up to 3 successful broods per season (Chilton et al. 1995) and have a modal clutch size of 4 eggs in our population (J. W. Rivers personal observations). Therefore, the nest cycle we used for sparrows in our study included 3 days for egg laying, 12 days for incubation (which included the last day of egg laying), and 10 days for rearing nestlings (Baicich and Harrison 1997). We also considered the dependent period for fledglings to be 30 days based on previous studies (Chilton et al. 1995).

We restricted our assessment of post-fledging survival to control and moderate herbicide application treatments, with the moderate treatment reflecting the most common approach to vegetation control in our study region, and we monitored tagged fledglings until death or emigration from our study area. To accomplish this, we visited nests within 2 days of the expected fledging date to attach a lightweight VHF radio tag (tag mass ≤ 0.5 g, average = 2.6% of nestling body mass; PicoPip Ag317, BioTrack, UK). We selected 1 nestling in the middle of the brood size hierarchy for tag attachment using the harness method (Rappole and Tipton 1991). After affixing the tag, we returned the nestling to its nest and immediately left the area. We attempted to locate each tagged sparrow on the day following transmitter attachment and every 1–2 days thereafter to assess its status (alive/dead). During each tracking session, we took care to minimize disturbance on our approach. We marked the initial location for each sparrow with a GPS and returned later, typically within a week, to quantify vegetation (see below). Following our previous work with songbird fledgling survival in early-successional forests (Rivers et al. 2012), we considered an individual to have died if (1) we discovered all or part of its carcass with the radio tag, (2) we found its radio signal emanating from a microhabitat deemed unsuitable for fledgling sparrows (e.g., underground burrow), or (3) the tag was undetected, reflecting a long-distance movement that was inconsistent with age-specific movement ability. When an individual initially was missing during a tracking period, we undertook 3 consecutive searches from high points surrounding our study area to maximize the potential for detecting radio signals. For individuals that were not encountered during these extensive searches and were old enough to move long distances, we considered the individual to have survived and dispersed from the natal area given that signals from radio tags were detected well beyond the boundaries of our study plots. The majority of the tagged sparrows we tracked were

eventually detected as mortality events (see Results), suggesting that our approach was sound for relocating birds when they were present, and that we were unlikely to incorrectly assign dispersal to birds that had died.

Quantification of Vegetation Cover

To quantify the efficacy of herbicide treatments on stand-scale vegetation cover, we established 3 randomly selected sampling points on each stand that were each located >50 m from the stand edge. Each sampling point had three 3 m radius circular subplots associated with it, for a total of 9 subplots sampled per stand. We located the center of each subplot 20 m from the sampling point, with 120° of separation between subplots to maximize stand coverage. On each subplot on each stand, we estimated vegetation cover by summing the extent of live vegetation provided by each plant species and functional group; unlike our measures at nest sites and fledgling locations (see below), we took a single estimate across all vertical strata. Next, we took the average value across the 3 subplots at each sampling point, and then averaged across the 3 sampling points with each stand for a single stand-scale average.

Microhabitats with greater concealment from vegetation are expected to have an increased probability of nest survival (Martin and Roper 1988, Martin 1992; but see Borgmann and Conway 2015); therefore, we quantified nest vegetation around each sparrow nest at 2 distinct spatial scales (Martin 1992). First, we quantified vegetation cover in a 3 m radius circular plot centered on the nest, which we refer to as nest-patch concealment, by visually estimating the amount of live vegetation cover provided by each plant species or functional group (i.e. forbs, ferns, and grasses) within each of 3 vertical strata (i.e. herb stratum [0–0.5 m], shrub stratum [0.5–2.0 m], and tree stratum [>2 m]) following our previous work (Ellis and Betts 2011, Betts et al. 2013). For analysis we summed cover values over all strata for all species and functional groups observed, which can result in cover values >100% when cover for a species/functional group overlaps in multiple strata. In addition, we measured vegetation cover immediately surrounding the nest, which we refer to as nest-site concealment, by visually estimating the amount of the nest concealed by live vegetation taken from (1) a single point that was 1 m above the ground and located directly above the nest, and (2) 4 points that were 1 m above the ground and 1 m from the nest in each of the cardinal directions; we used the average cover estimate from all 5 points for analysis and refer to this as nest-site concealment. All nest-based vegetation measurements were taken within 10 days of the nest finishing to ensure measures reflected vegetation present when the nest was available to fail (Borgmann et al. 2014). To evaluate the influence of vegetation-based covariates on post-fledging survival, we used the same approach for quantifying nest patch concealment to measure vegetative concealment at locations where live radio-tagged fledglings were located during tracking bouts.

During the first year of study (2013) we observed that some sparrow nests were hidden under woody debris that had been removed from felled trees during harvest activities (i.e. logging slash), and that fledgling sparrows often used slash as hiding cover shortly after leaving the nest. Therefore, in 2014 we measured slash in the vicinity of nests and at the locations where live radio-tagged fledglings were observed, and we predicted that nest and post-fledging survival rates would be higher with greater amounts of slash. We measured slash cover by visually estimating the coverage of slash in the same 3 m radius circle surrounding nests and fledging locations. We restricted our measurements to the herb stratum because most slash had settled to the forest floor by the time of our measurements (i.e. 4 yr post-harvest). We calculated mean slash depth from measurements at 4 points, one in each cardinal direction, located at the edge of the same 3 m radius plot. We did not restrict our measurements to slash of a particular diameter, as slash of all sizes appeared to be used for hiding cover (J. W. Rivers personal observation). Our initial analysis found that slash cover and slash depth were positively correlated ($r > 0.33$ across treatments), so we restricted our analysis to slash cover alone.

Analysis of Herbicide Treatments on Vegetation Cover

We assessed how herbicide treatments influenced stand-scale vegetation cover with an analytical model that contained year (2 levels: 2013, 2014), treatment (4 levels: light, moderate, and intensive herbicide application, and no-spray control), and a year*treatment interaction as fixed effects, with study block, stand, and a block*year interaction as random effects. Similarly, we constructed separate models to examine how herbicide treatments influenced the extent of vegetation cover as measured by nest-patch concealment and nest-site concealment. For both measures, our model contained treatment (4 levels), year of study (2 levels), and a treatment*year interaction as fixed effects; nest initiation date (continuous) as a covariate; and study block, a block*year interaction, a block*treatment interaction, and a year*block*treatment interaction as random effects.

Analysis of Nest Survival and Post-fledging Survival

We modeled daily survival rates of sparrow nests with the logistic exposure method of Shaffer (2004) using PROC GENMOD in SAS 9.4 (SAS Institute, Cary, North Carolina, USA). This approach is well suited for studies that evaluate nest survival when exposure periods vary, as they did in our study, and it has the additional benefit of being able to evaluate the influence of design-based (e.g., experimental treatments) and time-varying covariates (e.g., day of year) on survival (Shaffer 2004, Grant et al. 2005, Shaffer

and Thompson 2007). We initially fitted a design-based model for daily survival rate that included experimental treatment (4 levels), year of study (2 levels), study block (4 levels), and a treatment*year interaction to assess the consistency of treatment response across time as fixed effects. In addition to variables incorporated into the experimental design, daily survival rates can also be influenced by 2 time-dependent covariates: nest age and nest initiation date (Shaffer 2004, Grant et al. 2005). There are several plausible linear and nonlinear relationships between daily survival rates of songbird nests (Grant et al. 2005), so we initially used a model selection approach that incorporated Akaike information criteria (AIC) to determine the best-fitting model from a set of candidate models that included different combinations of nest age and nest initiation date; the top model contained a linear effect for nest age and nest initiation date (Supplemental Material Appendix B). We did not include random effects in any of our nest survival models because constructing survival models with random effects is inappropriate when nests are discovered after initiation, as they were in our study, because some nests in the population fail prior to discovery by researchers and leads to a nonrandom subset of nests available for modeling survival; see Heisey et al. (2007) for a detailed discussion of this issue.

In addition to using a design-based model, we also constructed 2 vegetation-based covariate models to evaluate how nest-patch concealment and nest-site concealment were linked to daily survival rate of sparrow nests. Herbicides target nest vegetation, so the vegetation covariate model did not include the confounding herbicide treatment effect. Thus, our vegetation cover covariate model included year (2 levels), study block (4 levels), linear effect of nest age (continuous), linear effect of nest initiation date (continuous), nest-patch concealment (continuous), and nest-site concealment (continuous). We included both nest-based vegetation measures in this model because these 2 measurements may have different influences on nest survival and were uncorrelated within each of our 4 treatments (all $r < 0.14$). We constructed a second covariate model to evaluate whether slash cover was linked to nest daily survival rate. Slash measurements were taken in 2014 only, so our slash cover covariate model included treatment (4 levels), study block (4 levels), linear effect of nest age (continuous), linear effect of nest initiation date (continuous), and slash cover (continuous). For both covariate models we included a linear effect of nest age and a linear effect of nest initiation date because they were included in the best-fitting model; we provide a summary of all models used to evaluate nest survival and post-fledging survival relative to experimental treatments and covariates (Supplemental Material Appendix B).

To evaluate sparrow post-fledging survival, we used Cox proportional hazards modeling because this approach does not assume a specific hazard function and allows for time-varying covariates (Murray 2006). We used PROC PHREG in SAS 9.4 to construct a design-based model whose response variable was the number of days of exposure and had experimental treatment (2 levels: moderate herbicide application, no-spray control), year (2 levels), and date of tag deployment (continuous) as fixed effects. In addition, we also constructed 2 separate vegetation-based covariate models to evaluate the link between vegetation and post-fledging survival. In the first model, we included year (2 levels), date of tag deployment (continuous), and vegetation cover at fledgling locations (continuous) as fixed effects. In the second model, which was restricted to 2014, we included date of tag deployment (continuous), and total slash cover at fledgling locations (continuous) as fixed effects. Unless otherwise noted, we report means as marginal least squares means and their associated 95% confidence intervals (CIs) and effect sizes as marginal model-derived parameter estimates (β) and their associated 95% CIs, both of which are taken at the mean value for each covariate within each model.

RESULTS

Over 2 yr of study we located and monitored the fates of 761 sparrow nests, resulting in 3,712 survival intervals. Predation was attributed as the causal factor to 91% of failed nests. More nests were found in 2014 ($n = 489$) than in 2013 ($n = 272$), although the number of nests observed per study block was generally similar when both seasons were combined (range: 168–223 nests per block).

Influence of Herbicide Treatments on Vegetation Cover

As expected, herbicide application led to changes in vegetation cover across our experimental treatment gradient: we detected a treatment effect on the amount of stand-scale vegetation cover whereby vegetation cover was reduced as herbicide intensity increased ($F = 7.59$, df = 3 and 9, $P = 0.008$), with no evidence of an effect of year ($F = 1.57$, df = 1 and 3, $P = 0.299$) or a treatment*year interaction ($F = 0.65$, df = 3 and 9, $P = 0.602$; Table 1). When assessing treatment effects on nest-patch concealment we also found evidence of a treatment effect ($F = 7.43$, df = 3 and 9, $P = 0.008$), with no evidence of an effect of year ($F = 0.22$, df = 1 and 3, $P = 0.670$) or a treatment*year interaction ($F = 0.88$, df = 3 and 9, $P = 0.489$); the amount of nest-patch concealment decreased with increasing herbicide intensity, with some recovery in the intensive treatment in the second year (Figure 2A). In contrast, when evaluating nest-site concealment we did not detect an effect of treatment ($F = 1.59$, df = 3 and 9, $P = 0.259$), nor did we find

TABLE 1. Response of vegetation cover to experimental treatments across experimental herbicide gradient for 2013 and 2014, illustrating the reduction in stand-scale vegetation across study sites.

	2013		2014	
Experimental treatment	Mean stand-scale vegetation cover (%)	95% CI	Mean stand-scale vegetation cover (%)	95% CI
No-spray control	94.2	75.8, 112.6	95.2	76.9, 113.6
Light herbicide	78.5	60.2, 96.9	82.6	64.2, 100.9
Moderate herbicide	64.2	45.9, 82.6	79.3	61.0, 97.7
Intensive herbicide	51.1	32.8, 69.5	54.9	36.6, 73.3

evidence of a year (F = 4.40, df = 1 and 3, P = 0.127) or a treatment*year (F = 0.71, df = 3 and 9, P = 0.568; Figure 2B) interaction.

Influence of Herbicide Treatments and Covariates on Nest Survival

In our design-based model, we detected no difference in the daily survival rates of nests located across the gradient of experimental herbicide application (χ^2 = 3.56, P = 0.313) although daily survival rates were lower in the second year of study across all treatments (χ^2 = 12.83, P < 0.001), with no treatment*year interaction (χ^2 = 0.38, P = 0.944; Figure 3). Effect sizes for the difference in daily survival rate between the no-spray control and herbicide treatments overlapped for all paired comparisons in both years of study (Table 2). In addition, we found no evidence that daily survival rate was linked to measurements of vegetation or slash in the vicinity of nests. In our vegetation covariate model we did not detect associations between daily survival rate and either nest-patch concealment (β = 0.00 [95% CI: 0.00, 0.00], χ^2 = 0.52, P = 0.471) or nest-site concealment (β = 0.01 [95% CI: 0.00, 0.01], χ^2 = 3.27, P = 0.071). Similarly, we found no evidence for a relationship between daily survival rate and slash cover (β = 0.00 [95% CI: 0.00, 0.00], χ^2 = 0.13, P = 0.717).

With respect to time-varying covariates, we did find evidence for a negative relationship between daily survival rate for mean nest age (β = −0.04 [95% CI: −0.06, −0.02], χ^2 = 22.87, P < 0.001) and for mean nest initiation date (β = −0.01 [95% CI: −0.02, 0.00], χ^2 = 10.25, P = 0.001). When nest initiation date was held constant, we found daily survival rates for all treatments declined with nest age during the laying and incubation periods, and the rate of decline was steeper during the nestling period (Table 3, Supplemental Material Appendix C). We observed a similar pattern for nest initiation date when nest age was held constant, as daily survival rate for all treatments exhibited a gradual, constant decline across the breeding season (Supplemental Material Appendix C). Period survival estimates for treatments when daily survival was held constant ranged from 0.438 to 0.556 in 2013, and 0.304 to 0.402 in 2014 (Table 4).

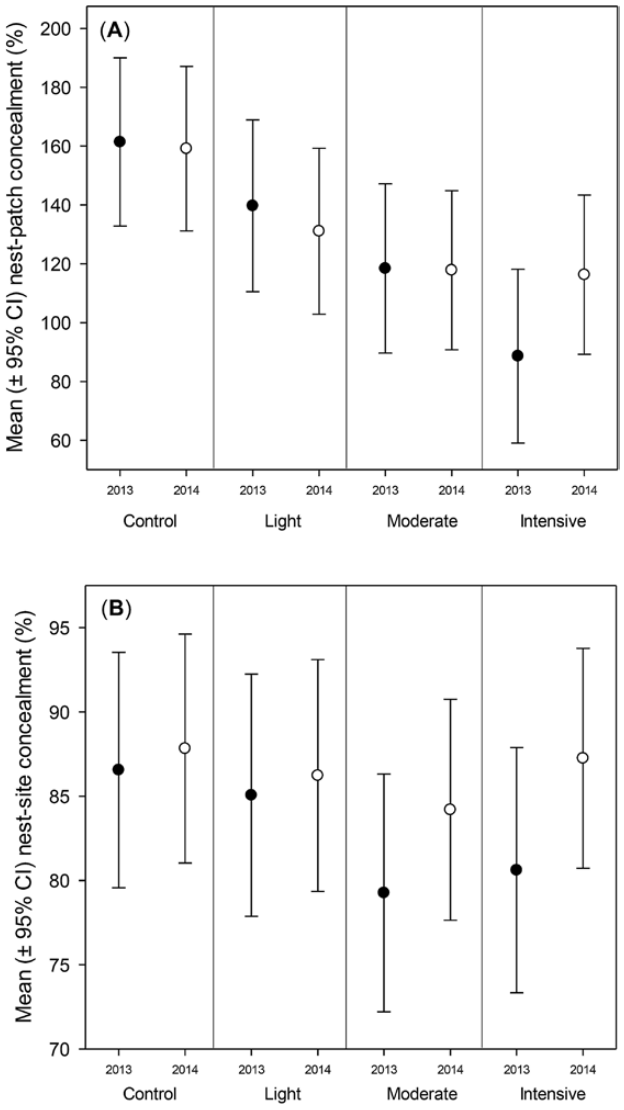

FIGURE 2. (**A**) Mean (±95% CI) nest-patch vegetation concealment and (**B**) nest-site vegetation concealment estimates for nests of White-crowned Sparrows across an experimental gradient of herbicide application intensity. Note that nest-patch concealment measures can exceed 100% when cover estimates for species and/or functional groups overlapped across multiple strata.

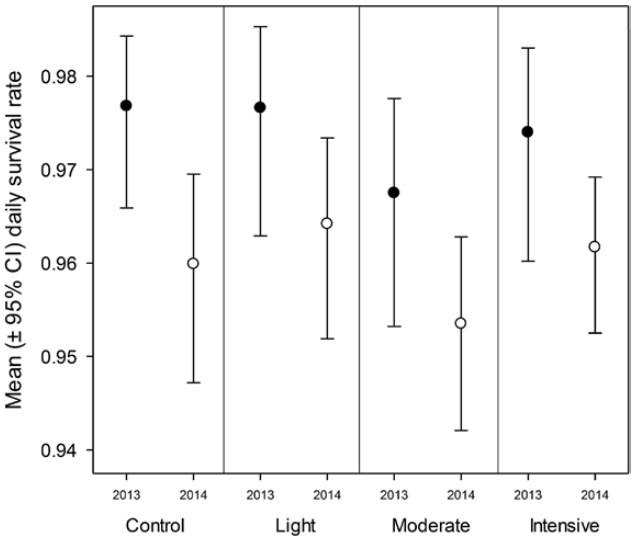

FIGURE 3. Mean (±95% CI) daily survival rate estimates for nests of the White-crowned Sparrow across an experimental gradient of herbicide application intensity.

TABLE 2. Contrasts with control stands for parameter estimates (β) and associated 95% confidence interval (CIs) for daily survival rate of White-crowned Sparrow nests in each year of study for each of 3 levels of experimental herbicide treatment.

Year	Contrast with No-spray control	β	95% CI	*P*
2013	Light herbicide	0.01	−0.60, 0.62	0.977
	Moderate herbicide	0.35	−0.20, 0.89	0.213
	Intensive herbicide	0.12	−0.47, 0.71	0.693
2014	Light herbicide	−0.12	−0.54, 0.30	0.580
	Moderate herbicide	0.15	−0.21, 0.52	0.413
	Intensive herbicide	−0.05	−0.41, 0.31	0.790

Influence of Herbicide Treatments and Covariates on Post-fledging Survival

We assessed survival in 70 fledglings, with roughly half of the individuals divided into each of the 2 treatment groups (no-spray control: n = 37; moderate herbicide treatment: n = 33). In our design-based model we found no evidence for a difference between post-fledging survival relative to these 2 treatments (β = 0.48 [95% CI: −0.18, 1.14], hazard ratio = 1.62 [95% CI: 0.84, 3.13], χ^2 = 2.04, P = 0.154; Figure 4) or year (β = −0.47 [95% CI: −1.15, 0.21], hazard ratio = 0.62 [95% CI: 0.31, 1.24], χ^2 = 1.84, P = 0.175). However, we did detect a positive relationship between the date of tag deployment and survival (β = 0.19 [95% CI: 0.10, 0.27], hazard ratio = 1.20 [95% CI: 1.12, 1.32], χ^2 = 20.49, P < 0.001) indicating that the hazard rate increased with time across the breeding season. Post-fledging survival on control stands was consistently lower than that of moderate herbicide stands across the observed range of exposure days (Figure 4), indicating the proportional hazards assumption was met.

In our vegetation-based covariate model we found that post-fledging survival did not appear to be influenced by year (β = −0.11 [95% CI: −1.77, 1.55], hazard ratio = 0.90 [95% CI: 0.17, 4.72], χ^2 = 0.02, P = 0.898), date of tag deployment (β = 0.05 [95% CI: −0.07, 0.16], hazard ratio = 1.05 [95% CI: 0.93, 1.18], χ^2 = 0.64, P = 0.425), or vegetation cover (β = 0.01 [95% CI: 0.00, 0.02], hazard ratio = 1.01 [95% CI: 1.00, 1.02], χ^2 = 1.23, P = 0.268). Similarly, in the model that tested the influence of slash on post-fledging survival we found no effect of date of tag deployment (β = 0.13 [95% CI: −0.16, 0.41], hazard ratio = 1.13 [95% CI: 0.85, 1.51], χ^2 = 0.73, P = 0.392) or slash cover (β = −0.06 [95% CI: −0.38, 0.25], hazard ratio = 0.94 [95% CI: 0.69, 1.28], χ^2 = 0.16, P = 0.690).

DISCUSSION

Our study revealed 3 important findings regarding vegetation cover and its relationship to sparrow nest survival. First, we were able to create a strong divergence in the extent of stand-scale vegetation cover during the course of our study through experimental herbicide treatments. Second, we detected treatment differences in nest-patch concealment, but we did not find evidence for a treatment difference for nest-site concealment. Finally, we found no relationship between nest survival and either measure of vegetation concealment measured in the vicinity of active nests. The great majority of nests failed due to predation even though herbicide-driven reduction in vegetation was not linked to nest survival, suggesting that the key nest predator(s) in our system may have been uninfluenced by vegetation concealment at the scale of the stand and the nest patch. Which predator group(s) was responsible for this pattern is unclear, but one possibility is that predation was driven by small-bodied nest predators (e.g., small mammals, snakes) that are themselves preyed upon by higher trophic level predators (e.g., raptors). Under this scenario, the dense vegetation cover we recorded at nest sites may have provided small-bodied nest predators hiding cover when searching for and preying upon sparrow nests, ultimately benefiting them via a reduction in predation risk. Alternatively, predator populations and behavior may have been unaffected by herbicide treatment, and nest survival reflected sparrows finding adequate nest cover in all treatments. Although we were unable to quantify nest predators, 2 lines of evidence suggest that small-bodied predators may have been important mortality agents in our study. First, observations made during the course of field work indicated that small mammals (e.g., chipmunks [*Tamias* spp.]) and snakes, especially the red-sided garter snake (*Thamnophis sirtalis*), were present

TABLE 3. Candidate models for modeling 2 time-dependent covariates (i.e. nest age, nest initiation date) on daily survival rate of White-crowned Sparrow nests in western Oregon, USA. Models are ranked according to differences in Akaike Information Criterion (**Δ**AIC). Note that linear terms were also included when a quadratic term was added to a model.

Model	*K* [a]	AIC	ΔAIC	w_i [b]	ER [c]
base model + nest age + date	8	2274.75	0.00	0.373	1.000
base model + nest age^2 + date	9	2275.11	0.35	0.313	1.193
base model + nest age + date^2	9	2276.32	1.56	0.171	2.186
base model + nest age^2+ date^2	10	2276.76	2.01	0.137	2.725
base model + nest age^2	8	2282.90	8.15	0.006	58.874
base model + nest age	7	2283.00	8.25	0.006	61.834
base model + date	7	2295.62	20.87	0.000	>34,000
base model + date^2	8	2296.59	21.84	0.000	>55,000
base model[d]	6	2311.21	36.45	0.000	>820,000,000

[a] Denotes number of parameters in model.
[b] Relative likelihood of the current model (*i*) based on AIC value.
[c] Evidence ratio.
[d] Base model (i.e. null model): year + treatment + year*treatment + block.

TABLE 4. Period survival for White-crowned Sparrow nests in western Oregon, USA. Estimates assumed constant survival across the nesting cycle and were calculated by taking daily survival rates across the entire 25-day nesting cycle (consisting of 3 days for egg laying, 12 days for incubation, and 10 days for rearing nestlings following Baicich and Harrison [1997]).

Year	Treatment	Period survival	95% CI
2013	Control	0.556	0.420, 0.673
	Light	0.553	0.389, 0.691
	Moderate	0.438	0.302, 0.568
	Intensive	0.518	0.362, 0.651
2014	Control	0.359	0.258, 0.461
	Light	0.402	0.292, 0.510
	Moderate	0.304	0.225, 0.388
	Intensive	0.377	0.296, 0.457

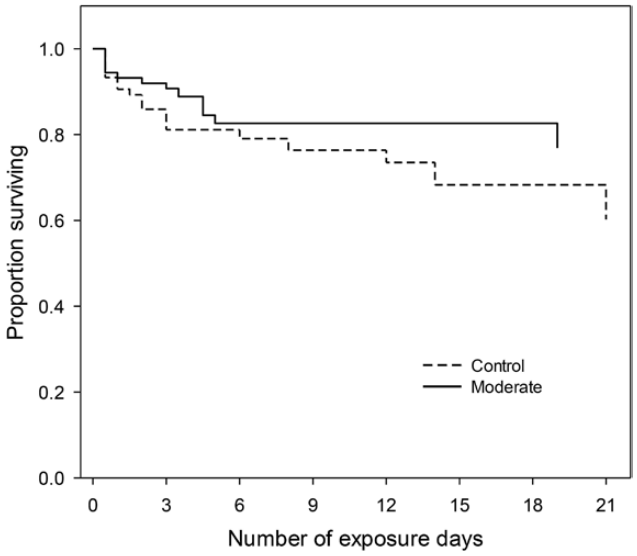

FIGURE 4. Estimated survival functions of post-fledging White-crowned Sparrows raised in no-spray control stands (dashed line, $n = 37$) or in stands subjected to moderate herbicide treatments (solid line, $n = 33$). Time-dependent covariates (i.e. year, date of tag deployment) were held at their average values for both survival curves.

on many of the stands throughout the summer breeding season. Both small mammals and snakes are important predators of songbird nests and fledglings (Schmidt et al. 2001, Weatherhead and Blouin-Demers 2004, DeGregorio et al. 2014), including sparrows and other songbird species nesting in early-successional managed conifer forests in our study area (James et al. 1983, Morton et al. 1993, Rivers et al. 2012). Second, small mammals are common in conifer forests of the Oregon Coast Range where we conducted our study (Morrison and Anthony 1989, Cole et al. 1998), and populations of some species in this region (e.g., *Peromyscus* spp.) are known to increase after clearcut harvest in regenerating conifer forests (Tevis 1956, Gashwiler 1970, Sullivan 1979). That we found lower sparrow nest survival in the second year of study across all treatments is consistent with the idea that populations of small-bodied predators may have been increasing on stands through time, leading to increased rates of nest predation. Although we are forced to speculate on predator identity, we can state with certainty that nest failure on our study sites was driven by nest predators. Therefore, future studies of herbicide treatment effects on nest predators will be valuable to better understand constraints on songbird productivity in early-successional conifer forests.

That sparrow nest survival was not linked to either nest-patch or nest-site vegetation measures was unexpected, as vegetation around active nests has been shown to have an important influence on nest survival in some systems by decreasing search efficiency of predators (Martin et al. 1988; Martin 1992, 1995). Nevertheless, our results are concordant with recent work on sparrows that found no

link between nest survival and vegetation measures (Porzig et al. 2018). That research was conducted in mixed shrub and grassland habitats in coastal California (Porzig et al. 2018), so it may be that nest vegetation is generally unassociated with nest survival in sparrows. In addition to studies of sparrows, many empirical studies have failed to detect a relationship between songbird nest survival and vegetation concealment (reviewed in Borgmann and Conway 2015). Several of the factors thought to explain this inconsistent relationship are unlikely to be relevant in our study system (e.g., mistimed nest vegetation measurements, male plumage brightness) so it remains unclear which factor(s) best explain(s) the lack of relationship between nest vegetation and nest survival we found.

Our results contrast with the only other experimental study on herbicides and songbird demography in conifer forests, which found negative effects of herbicide application and thinning on nest success (Easton and Martin 2002). The pronounced differences in time since harvest between when that study was undertaken relative to our work (11–22 yr post-harvest vs. 3–4 yr post-harvest) and the rapid differences in vegetation succession that ensue shortly after harvest occurs (Stokely et al. 2018) together suggest the 2 systems may have been fundamentally different by the time herbicide response was tested. Thus, it is perhaps not surprising that the demographic response to herbicides differed between the studies. What was worth noting about our study, however, was that sparrows were able to locate nest sites that contained high amounts of vegetation concealment on all of our study sites, regardless of the level of herbicide intensity. Recent work in similar conifer forest has found that a relatively small amount of broadleaf hardwood cover was linked to significant increases in richness and abundance of early-successional birds in plantation forests (Ellis and Betts 2011), so it appears that even small changes in the amount of competing vegetation cover may provide benefits to birds that require broadleaf plants and other vegetation types that are targeted by herbicides. This finding is important for informing management actions because it indicates that stands subjected to herbicide application, even those that are well within what is typically implemented as part of intensive forest management activities, can still provide nesting habitat for sparrows and other early-successional bird species (Betts et al. 2013, Kroll et al. 2017).

We found that post-fledging survival rates during the dependent period were not linked to either herbicide treatment or vegetation measures. Songbird post-fledging survival rates are typically low across species (Cox et al. 2014) including those that nest in early-successional conifer forests (Rivers et al. 2012), and this is especially true during the initial 2–3 weeks that immediately follow fledging from the nest. In turn, such low survival rates may make it hard to detect treatment differences. In line with this idea, a recent review of fledgling survival rates found mixed support for the influence of habitat on post-fledging survival (Cox et al. 2014), even among different studies that used similar radio-tagging techniques to monitor post-fledging survival within the same species. This finding indicates that system-specific factors appear to have a particularly strong influence on fledgling survival rates, and those factors may be more important than traditional habitat measures such as vegetation concealment. Of note, our previous work on the Swainson's Thrush (*Catharus ustulatus*) in early-successional conifer forests also found low fledgling survival rates and no link between survival and vegetation cover (Rivers et al. 2012). Thus, it may be that vegetation cover plays a lesser role in songbird fledgling survival within managed conifer forests for reasons currently unknown.

Conservation concern has been raised for decades about early-successional forests due in large part to long-term population declines of organisms that depend on these habitats during critical periods of their life cycle (Thompson and DeGraaf 2001, King et al. 2011, Swanson et al. 2011, Kwit et al. 2014, Swanson et al. 2014). A number of bird species associated with early-successional forest have undergone strong and consistent population declines over the last several decades (Betts et al. 2010, 2013; King and Schlossberg 2014), including those that require broadleaf vegetation that is targeted by herbicide application (Hagar et al. 2007, Betts et al. 2010, Ellis and Betts 2011). These declines have coincided with an overall decrease in the quantity and complexity of early-successional forest on the landscape (Kennedy and Spies 2005, Thomas et al. 2006, King and Schlossberg 2014), including a truncation of the period during which habitat conditions are suitable for early-successional obligates. Our study revealed that, in sparrows, the 2 vital rates that together comprise reproductive success were uninfluenced by changes in vegetation due to herbicide intensity. Additional work in this sparrow population has found no influence of herbicide treatments to offspring sex ratio (Rivers et al. 2017), a demographic trait generally influenced by conditions during development (Trivers and Willard 1973, Pike and Petrie 2003). Nevertheless, not all declining songbird species share the same specific habitat requirements as sparrows and therefore may exhibit different responses to herbicide application intensity. For example, leaf-gleaning species appear to be most strongly influenced by herbicide treatments that reduce broadleaf cover that is used for obtaining food resources during nesting (Betts et al. 2013, Kroll et al. 2017). Therefore, additional research on the demographic response of other species is needed to evaluate the generality of our results and to explore how management actions can be tailored to suit the needs of other declining bird species that require early-successional forest.

ACKNOWLEDGMENTS

We thank C. Adlam, T. Barron, J. Bailey, H. Beyl, S. Campbell, B. Cooney, G. Cummins, S. Doorly, E. Eve, D. Ferraro, C. Fitzmorris, N. Garlick, B. Hardt, R. Hepner, K. Jones, S. Jordan, E. Keyes, C. Loucks, L. Mangan, N. Marcy, D. Millican, A. Muniz, L. Natola, E. Pokrivka, J. Powell, T. Stokely, N. Volpe, K. Wilson, E. White, and K. Zummo for their assistance in the field; T. Shaffer for his thoughtful discussion of nest survival modeling, and J. Bakke for helpful feedback. Access to study sites as well as cooperation in implementing the experimental treatments was granted by Weyerhaeuser, Hancock Forest Management, the Oregon Department of Forestry, and Plum Creek Timber.

Funding statement: Research funding was provided by grants from the USDA, Agriculture Food and Research Initiative (AFRI-2009-04457, AFRI-2011-68005-30416), the National Council for Air and Stream Improvement, the Oregon State University Institute for Working Forest Landscapes, the Institute for Working Forest Landscapes Research Chair in Forest Biodiversity Research, and the Fish and Wildlife Habitat in Managed Forests Research Program in the College of Forestry at Oregon State University.

Ethics statement: All permitted activities described herein were carried out under the auspices of approved institutional, state, and federal research permits.

Author contributions: J.W.R. and M.G.B conceived the original idea for the project, with J.W.R. supervising the research and M.G.B securing most of the research funding. Methods were developed by all authors. J.W.R. conducted the research, and J.W.R and C.J.S. analyzed data with input from M.G.B. J.W.R. wrote the paper with input from all authors.

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