Response of corvid nest predators to thinning: implications for balancing short- and long-term goals for restoration of forest habitat

Joan C. Hagar 1,*, Theodore Owen 2, Thomas K. Stevens 3 and Lorraine K. Waianuhea 4,5

1 U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 2 Western EcoSystems Technology, Inc., 3 Department of Forest Resources, University of Minnesota, 4 Department of Integrative Biology, Oregon State University, Corvallis, OR, USA, 5 Department of Biology, University of Hawaii at Manoa, Honolulu, HI, USA

ABSTRACT. Forest thinning on public lands in the Pacific Northwest USA is an important tool for restoring diversity in forest stands with a legacy of simplified structure from decades of intensive management for timber production. A primary application of thinning in young (< 50-year-old) stands is to accelerate forest development to mitigate loss of late-seral habitat to decades of logging. However, thinning may have short-term negative effects for some species associated with mature forest that are expected to benefit from the practice over the long term. An increased risk of nest predation is a primary concern to managers charged with stewardship of habitat for the federally threatened Marbled Murrelet (Brachyramphus marmoratus), a species that nests in older forests. Predation by corvids is the greatest cause of nest failure for the Marbled Murrelet, and corvids are known to respond positively to forest disturbance, but quantitative information is lacking on the potential impacts of thinning on risk of nest predation. We investigated the response of two common corvid nest predators, Steller’s Jay (Cyanocitta stelleri) and Canada Jay (Perisoreus canadensis), to variation in thinning intensity in young forest (< 50 years old) using data from a long-term silviculture experiment. We used a Before-After-Control-Impact (BACI) design, linear mixed modeling, and occupancy modeling to quantify differences in corvid observation rates among varying levels of thinning intensity, and to assess changes in jay response over more than a decade following thinning. We found an increase in observation rates of both species in the heavily thinned treatment during the first 5 to 7 years following thinning, and some evidence of a short-term increase in Steller’s Jay activity in the thinning-with-gaps treatment. Neither jay species responded to the least intensive thinning treatment, which reduced average canopy cover by < 30%. By approximately a decade after thinning, observation rates of jays did not differ between unthinned controls and any of the thinning treatments. Incorporating our quantitative information into landscape-level planning can help managers balance short- and long-term conservation goals.

Réaction de corvidés prédateurs de nids à l’éclaircie : répercussions pour obtenir un équilibre entre les objectifs à court et à long termes de la restauration de l’habitat forestier

RÉSUMÉ. L’éclaircie forestière sur les terres publiques du nord-ouest des États-Unis est un outil important visant à restaurer la diversité dans les peuplements forestiers dont la structure a été simplifiée par des décennies d’aménagement intensif destiné à la production de bois. L’un des principaux objectifs de l’éclaircie de jeunes peuplements (< 50 ans) est d’accélérer la croissance de la forêt afin d’atténuer la perte d’habitat de stades successiellelement avancés attribuable à des décennies d’exploitation forestière. Cependant, l’éclaircie peut avoir des effets négatifs à court terme pour certaines espèces associées aux forêts matures qui devraient bénéficier de cette pratique à long terme. Le risque accru de prédation des nids est une préoccupation majeure pour les gestionnaires chargés de l’intendance de l’habitat du Guillemot marbré (Brachyramphus marmoratus), espèce menacée au niveau fédéral, qui niche dans les vieilles forêts. La prédation par les corvidés est la principale cause d’échec de la nidification du Guillemot marbré, et on sait que les corvidés réагissent positivement aux perturbations forestières, mais on manque d’informations quantitatives sur l’impact potentiel des éclaircies sur le risque de prédation des nids. Nous avons étudié la réaction de deux corvidés communs prédateurs de nids, le Geai de Steller (Cyanocitta stelleri) et le Mésangeai du Canada (Perisoreus canadensis), à la variation de l’intensité de l’éclaircie dans les jeunes forêts (< 50 ans) au moyen de données d’une expérience de sylviculture à long terme. Nous avons utilisé une approche BACI (before-after control-impact), une modélisation linéaire à effets mixtes et une modélisation de la présence pour quantifier la différence du taux d’observation des corvidés selon les divers niveaux d’intensité d’éclaircie, et évaluer les changements de réaction des geais sur plus d’une décennie après l’éclaircie. Nous avons constaté une augmentation du taux d’observation des deux espèces là où il y avait eu un traitement intense d’éclaircie au cours des 5 à 7 années suivant l’éclaircie, et quelques indications d’une augmentation à court terme de l’activité du Geai de Steller dans le traitement d’éclaircie avec trouées. Aucun des deux geais n’a réagi au traitement d’éclaircie le moins intensif, qui a réduit la voûte forestière moyenne de moins de 30 %. Environ dix ans après l’éclaircie, le taux d’observation des geais ne différait pas entre les traitements témoins non éclaircis et l’un ou l’autre des traitements d’éclaircie. L’intégration de nos informations quantitatives dans la planification au niveau du paysage peut aider les gestionnaires à équilibrer les objectifs de conservation à court et à long termes. 

Key Words: conservation; corvids; Cyanocitta stelleri; forest management; forest thinning; threatened species; nest predation; Perisoreus canadensis

Corresponding author: Joan C. Hagar, joan_hagar@usgs.gov
INTRODUCTION
Since the inception of the Northwest Forest Plan (NWFP) in 1994, a major goal of forest management on public lands in the Pacific Northwest has been to reverse population declines of species associated with old-growth forest through protection and restoration of their habitat (USDA and USDI 1994). Logging practiced since European settlement reduced the area of old-growth forest, and subsequent intensive management left a legacy of homogeneously structured, biologically simplified conifer plantations to dominate the landscape (Spies et al. 2018). Arrested growth rates and patterns of structural development in these dense plantations suggest that many are unlikely to ever achieve the heterogeneity characteristic of old-growth forest (Tappeiner et al. 1997, Poage and Tappeiner 2002). Structural features important for late-successional species that are unlikely or slow to develop from dense plantations include multiple canopy layers, diverse understory, and the large-diameter, horizontal limbs used as nesting platforms by some old forest species (USDA and USDI 1994, Hamer and Nelson 1995, Linnell et al. 2017). Forest managers have addressed the challenge of restoring structural and biological diversity to plantations through active management involving timber harvest, primarily commercial thinning. By reducing stand density, thinning increases growth rates of retained trees and promotes understory development through increased light availability on the forest floor. Adapted from its traditional use by silviculturists for maximizing commercial gain, the contemporary application of thinning addresses ecological goals of forest management under the hypothesis that density reduction will promote diversity (Carey et al. 1999, Wilson and Puettmann 2007) and hasten development of late-successional habitat (Latta and Montgomery 2004, Puettmann et al. 2016). Thinning has therefore been widely implemented at a range of intensities, with the intention of putting young plantations on developmental trajectories that will eventually provide habitat for species associated with characteristics of late-seral forests (USDA and USDI 1994, Singleton et al. 2023).

Although insufficient time has passed since implementation of the NWFP to assess the effectiveness of thinning as a tool for restoration of mature forest habitat, the short-term effects for wildlife include both positive and negative responses. Thinning that opens the canopy sufficiently to promote development of a productive understory benefits many species, including insect pollinators and birds (Hagar et al. 2004, Neill and Puettmann 2013). Species associated with older, closed-canopy forest may be negatively affected in the short term (Meiman et al. 2003, Hagar et al. 2004, Manning et al. 2012), but the trade-offs between the short-term, negative effects of canopy reduction and the resulting acceleration of tree growth are not well understood for these species. For example, the implementation of thinning at a range of intensities, resulting in variable densities of residual trees, is likely to both have immediate effects on ecological responses (Puettmann et al. 2013) and influence development of future stand structure (Verschuyl et al. 2011, Willis et al. 2018, Williams and Powers 2019). Potential short-term risks of thinning to species dependent on intact mature forest include increased access for predators (Wilson and Forsman 2013). Although this risk is expected to be mitigated over the long term with expansion of the crowns of residual trees and development of complex structure, information on duration of thinning effects on wildlife is limited. The potential of corvid predators to respond to disturbance and limit populations of their prey makes them a central concern in efforts to conserve threatened species (Liebezeit and George 2002). The response of corvids to thinning is of particular interest to forest managers charged with stewardship of habitat for the federally threatened Marbled Murrelet (Brachyramphus marmoratus), a species that nests in architecturally complex canopies of mature forest and is vulnerable to nest predation (Nelson 2020). Thinning is an important tool for accelerating the development of forest structure characteristic of murrelet nesting habitat, but short-term effects may exacerbate threats to population recovery. One of the most important factors limiting murrelet populations is nest failure caused by predation, with corvids (family Corvidae: crows, ravens, and jays) being the most documented predator of Marbled Murrelet nests (Nelson and Hamer 1995, Raphael et al. 2018). Although the direct effect of thinning on nest predators has not been well studied, positive responses of some corvid species to timber harvest and associated creation of abrupt forest edges suggests that thinning may attract them through increases in food resources and nesting sites (Ibarzabal and Desrochers 2004, Marzluff et al. 2004, Marzluff and Neatherlin 2006). By attracting corvid nest predators, openings in the forest canopy created by thinning are likely to decrease the buffering effect against the risk of nest predation provided by a uniform canopy of regenerating young forest adjacent to murrelet nest stands (Marzluff et al. 2000, Malt and Lank 2007).

Continuing declines of murrelet populations despite two decades of habitat protection and restoration under the NWFP suggest the need for a better understanding of the effects of forest management activities on factors influencing nesting success. A positive association between corvid density and risk of nest predation (Luginbuhl et al. 2001) combined with upward trends in the populations of four species of corvids known to be nest predators (Common Raven, Corvus corax; American Crow, Corvus brachyrhynchos; Canada Jay, Perisoreus canadensis; and Steller’s Jay, Cyanocittta stelleri) in the Northern Pacific Rainforest ecoregion over the past decade (Sauer et al. 2017) magnifies the threat of nest failure to murrelet recovery. Managers striving to balance the potential short-term risks of thinning against the long-term benefit of accelerating the development of mature forest habitats for species with rapidly declining populations, such as the Marbled Murrelet, are therefore in urgent need of information on the response of corvid nest predators to thinning.

The goal of our study was to inform the use of thinning as a forest restoration tool by assessing its potential to influence risk of nest failure through changes in the abundance of corvid nest predators. Under the NWFP, dense young plantations adjacent to older stands occupied by murrelets are candidates for thinning to accelerate development of complex structure, with the intention of expanding suitable nesting habitat in the long term. Managers considering this strategy need information to guide evaluation of the trade-offs between the potential short-term risks and the long-term benefits of thinning. Few datasets from within the nesting range of the Marbled Murrelet are available to address the question of corvid response to thinning. Therefore, we analyzed bird survey data from a long-term, experimental thinning study in the Cascade Range of Oregon to assess the response of Steller’s
and Canada Jays to thinning in conifer forests ecologically similar to those within the nesting range of the murrelet. We used a Before-After-Control-Impact (BACI) design to (1) quantify differences in corvid observation rates among stand-level treatments representing variation in thinning intensity; and (2) determine the influence of thinning intensity on the duration of corvid response up to 13 years following thinning.

**METHODS**

**Study area**

The Young Stand Thinning and Diversity Study (YSTDS; Manning and Friesen 2013) was located on the Willamette National Forest, within the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1988) on the western slope of the central Oregon Cascade Range. Sites were dominated by even-aged Douglas-fir (*Pseudotsuga menziesii*) plantations established after clearcutting mature forest. Following site preparation with broadcast burning and planting, sites had been pre-commercially thinned at approximately 15 years of age and were 30- to 45-years-old when YSTDS thinning began in 1994. Slopes ranged from 0 to 24%, and elevation ranged from 430 to 920 meters.

In addition to Douglas-fir, other tree species that comprised minor components of the overstory included western hemlock, western redcedar (*Thuja plicata*), bigleaf maple (*Acer macrophyllum*), and giant chinquapin (*Chrysolepis chrysophylla*). Dominant understory species included sword fern (*Polystichum munitum*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), Oregon grape (*Mahonia nervosa*), and Pacific rhododendron (*Rhododendron macrophyllum*).

Although the YSTDS study sites were located too far inland to be accessible to murrelets, we believe our results are representative of jay response to thinning in conifer forests of western Oregon because both jay species are common nest predators in conifer forests across the Pacific Northwest (Strickland and Ouellet 2020, Walker et al. 2020). The Steller's Jay is among the most abundant bird species in both the Coast Range and Cascade Ecoregions of Oregon (Carey et al. 1991, Gilbert and Allwine 1991), and although no consistent relationship between Steller’s Jay abundance and forest age or structure has been documented (Weikel 2003), the species is responsive to disturbance across its range (Sieving and Willson 1998, Brand and George 2001, Raphael et al. 2002). The Canada Jay is less common than the Steller’s, but its abundance is also similar between Coast Range and Cascade Ecoregions (Marshall et al. 2003). The broad patterns of occurrence and abundance of both species, combined with their opportunistic foraging habits, suggest that there is no reason to believe their response to thinning would differ between Coast Range and Cascade conifer forests. Furthermore, the avian assemblage co-occurring with both jay species is similar between Coast and Cascade conifer forests, as is the response of individual songbird species to thinning (Hayes et al. 2003, Hagar et al. 2004).

**Study design**

Four silvicultural treatments were applied to 30- to 45-year-old stands to test hypotheses about the effects of thinning on the developmental trajectories of stand structure (Table 1; Manning and Friesen 2013). In all thinning treatments, suppressed and intermediate trees were targeted for removal, to reduce competition and improve growth of the remaining dominant trees (Smith et al. 1997). The treatments were (1) a heavy thin (HT) resulting in a regular spacing of 125–137 trees per hectare (tpi; 50–55 trees per acre [tpa]); (2) a light thin (LT), approximating the timber industry standard, with 250–275 residual tpi (100–110 tpa), regularly spaced; (3) a light thin with gaps (LG), again with 250–275 tpi (100–110 tpa) but with an additional 20% of the stand area harvested to create 0.2-ha (1 acre) gaps, and (4) an unthinned control (CO). The study employed a BACI design (McDonald et al. 2000) with one replication of each treatment in each of 4 geographic blocks, for a total of 16 experimental units (i.e., “stands”; Fig. 1). Treatments were randomly assigned to stands within each block. Thinning was done at different times for each block, with all harvests completed between April 1995 and February 1997. Area of thinned stands ranged from 15 to 40 ha, with a mean of 27 ha; unthinned control stands were 30 to 53 ha, with a mean of 45 ha (Manning and Friesen 2013). Initial basal area and density of trees prior to treatment were similar among treatment units within blocks (Davis et al. 2007). Elevation of stands within a block generally differed by less than 240 m.

**Table 1**: Thinning treatments applied to 30- to 45-year-old conifer stands in the Young Stand Thinning and Diversity Study, Cascade Range, Oregon, USA.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Target tree density (Manning and Friesen 2013)</th>
<th>Associated hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light thin (LT)</td>
<td>300 trees per ha</td>
<td>Standard silvicultural practices will produce stand structure and composition more similar to old-growth over time more quickly than doing nothing at all.</td>
</tr>
<tr>
<td>Light thin with gaps (LG)</td>
<td>300 trees per ha; and 20% of the stand in 0.2 ha openings</td>
<td>Standard silvicultural practices modified to include gaps will produce spatial heterogeneity, with stand structure and composition more similar to old-growth over time more quickly than a standard silvicultural thinning.</td>
</tr>
<tr>
<td>Heavy thin (HT)</td>
<td>180 trees per ha</td>
<td>Rapid growth of trees and understory in response to open canopy will produce stand structure and composition more similar to old-growth over time more quickly than any other treatment.</td>
</tr>
<tr>
<td>Unthinned control (CO)</td>
<td>&gt; 650 trees per ha</td>
<td>Untreated stands will take the longest time to produce stand structure and composition similar to old-growth, if at all.</td>
</tr>
</tbody>
</table>

**Avian data collection**

Standard point count methodology (Ralph et al. 1995) was used to survey breeding birds at 3–5 stations in each of the 16 stands. Count stations were ≥ 75 m away from stand edges, road buffers, and riparian buffers, as well as ≥ 150 m away from each other. During the 10-min counting period at each station, surveyors...
Fig. 1. Map of study areas used to investigate corvid response to thinning on the Willamette National Forest, Oregon, USA from point count data collected May–July 1992–2007. The portion of the breeding range of the Marbled Murrelet (Brachyramphus marmoratus) in Oregon that is encompassed by Conservation Zone 3 (USFWS 1997) is shown in inset on lower left, outlined in red.

We tested for the effects of thinning on avian detectability (Dawson 2012, Hayes and Monfils 2015). Therefore, as a first step, we recorded the species of all individual birds observed as well as the estimated distance from the observer (Hagar et al. 2004). Each station was visited on 3–5 dates to collect avian point count data between mid-May and early July of each year of the study. Pre-treatment point counts were conducted 2 to 4 years before thinning, and post-treatment counts were conducted 1 to 13 years after thinning (Table 2). Three phases of the study were defined for analysis (Table 2): Pre-treatment (1992–1993; 2 to 4 years before thinning), Phase 1 (1997–2001; 1 to 7 years post thinning), and Phase 2 (2006–2007; 10 to 13 years post-thinning). Observers and number of observers varied by Phase (Table 2).

Data analysis
We used two separate modeling frameworks to resolve the problem of accounting for imperfect detection of jays given the larger size of corvid home ranges relative to the area surveyed during point counts. Canada Jay home ranges measure ~30 to 130 ha (Strickland and Ouellet 2020), whereas Steller’s Jay home range size averaged 80 ha in the Pacific Northwest (Marzluff et al. 2004); the average size of stands in our study, which contained 3–5 different point count locations, was 31 ha. Occupancy and N-mixture models, which rely on repeated surveys of a location and the assumption that the location is closed to animal movement between surveys, are strongly biased when the territory size of the species of interest is much larger than the survey unit (Efford and Dawson 2012, Hayes and Monfils 2015). Therefore, as a first step, we tested for the effects of thinning on avian detectability to determine whether accounting for changes in detectability due to the treatments and phases was necessary. To accomplish this, we used detection records of other species commonly recorded in this study that do not violate the closure assumption (home range sizes in these species are smaller than survey units) to create occupancy models that represent occurrence and detectability simultaneously. We selected 18 species (Appendix 1) that were the least likely of the species in our dataset to violate the closure assumption of an occupancy analysis and fit a community occupancy model using the R package spOccupancy (Doser et al. 2022). We used treatment, block, phase, and the interaction of treatment and phase for the occupancy covariates, and treatment, phase, and the interaction of treatment and phase for the detectability covariates.

We found no evidence of a difference in detection probability between the control treatment, pre-thinning phase and any other treatment-and-phase combination for the community of 18 species for which we assessed detectability (all 95% credible intervals contained 0). This community-level result indicated no need to account for differences in detection probability due to treatments and phases in the second modeling framework, a linear mixed models for jays.

Calculation of response variable
We used observation rates of corvid nest predators as an indicator of predation risk (Andren 1992, Vigallon and Marzluff 2005). We calculated observation rates for Steller’s and Canada Jays for each stand in each survey year as the total number of individuals observed divided by the number of surveys (survey stations * survey dates; see Table 3 for effort summaries). We computed the difference in observation rate of each species between treatments and CO as the response variable (hereafter, “difference in observation rate”) to assess treatment effects.

Statistical analysis
We used a linear mixed model approach via the R package nlme (Pinheiro et al. 2016) to assess the effect of treatment, phase, and the interaction of treatment and phase on difference in observation rates. Blocks and stands within blocks were treated as random effects in the model. We fit the model allowing for residual autocorrelation to account for repeated measurements on the same sites through time.

We used the package lsmeans version 2.27-62 (Lenth 2016) to perform pairwise comparisons of interest. Tukey’s method was used to control familywise error rate. Statistically significant differences were those that had Tukey adjusted 95% confidence intervals that did not include 0, because 0 indicated no difference in observation rate between CO and treatment. All analyses were conducted with R version 4.2.1 (R Core Team 2021).

RESULTS
Observations of both Steller’s and Canada Jays increased after thinning in all treatments, with strong evidence of an effect of thinning in the HT treatment for both species (95% confidence interval did not contain 0; Figs. 2 and 3). There was also some evidence of an effect in the LG treatment for Steller’s Jay (95% Phase 1 confidence interval barely contained 0; Fig. 2). The strongest effect was observed in the HT treatment during Phase 1, within 3 to 5 years of thinning (mean difference for Steller’s Jay...
Table 2. Timing of avian surveys relative to application of thinning treatments and observer variation among phases in the Young Stand Thinning and Diversity Study, Willamette National Forest, Oregon, USA. Time since thinning is approximate because thinning took place over 18 months.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Year</th>
<th>Time since thinning (approximate)</th>
<th>Observers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-treatment</td>
<td>1992–1993</td>
<td>2–4 years before</td>
<td>MH</td>
</tr>
<tr>
<td>[treatment applied]</td>
<td>August 1995–February 1997</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Phase 2</td>
<td>2006–2007</td>
<td>10–13 years</td>
<td>BS, JH</td>
</tr>
</tbody>
</table>

Table 3. Summary of number of corvid observations and survey effort (number of survey stations * number of survey dates) per phase per thinning treatment in the Young Stand Thinning and Diversity Study, Willamette National Forest, Oregon. Phases were: Pre-Treatment (1992–1993; 2 to 4 years before thinning), Phase 1 (1997–2001; 1 to 7 years post-thinning), and Phase 2 (2006–2007; 10 to 13 years post-thinning).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Steller’s Jay</th>
<th>Canada Jay</th>
<th>Survey effort (stations * survey dates)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>39</td>
<td>17</td>
<td>160</td>
</tr>
<tr>
<td>Phase 1</td>
<td>30</td>
<td>5</td>
<td>237</td>
</tr>
<tr>
<td>Phase 2</td>
<td>24</td>
<td>6</td>
<td>135</td>
</tr>
<tr>
<td>(Sub-total)</td>
<td>(93)</td>
<td>(28)</td>
<td>(532)</td>
</tr>
<tr>
<td>Light thin</td>
<td>Pre-treated</td>
<td>30</td>
<td>7</td>
</tr>
<tr>
<td>Phase 1</td>
<td>36</td>
<td>6</td>
<td>207</td>
</tr>
<tr>
<td>Phase 2</td>
<td>27</td>
<td>1</td>
<td>116</td>
</tr>
<tr>
<td>(Sub-total)</td>
<td>(93)</td>
<td>(14)</td>
<td>(483)</td>
</tr>
<tr>
<td>Light thin with gaps</td>
<td>Pre-treated</td>
<td>27</td>
<td>8</td>
</tr>
<tr>
<td>Phase 1</td>
<td>39</td>
<td>11</td>
<td>196</td>
</tr>
<tr>
<td>Phase 2</td>
<td>21</td>
<td>7</td>
<td>112</td>
</tr>
<tr>
<td>(Sub-total)</td>
<td>(87)</td>
<td>(26)</td>
<td>(467)</td>
</tr>
<tr>
<td>Heavy thin</td>
<td>Pre-treated</td>
<td>27</td>
<td>8</td>
</tr>
<tr>
<td>Phase 1</td>
<td>68</td>
<td>18</td>
<td>181</td>
</tr>
<tr>
<td>Phase 2</td>
<td>28</td>
<td>2</td>
<td>103</td>
</tr>
<tr>
<td>(Sub-total)</td>
<td>(123)</td>
<td>(28)</td>
<td>(443)</td>
</tr>
<tr>
<td>Totals</td>
<td>396</td>
<td>96</td>
<td>1925</td>
</tr>
</tbody>
</table>

between HT and CO = 0.312 observations/survey, p-value = 0.0085, Tukey-adjusted lsmeans; Fig. 2; mean difference for Canada Jay between HT and CO = 0.14 observations/survey, p-value = 0.001, Tukey-adjusted lsmeans; Fig. 3). The difference in Steller’s Jay observation rate between HT and CO during this time was statistically significant because the confidence interval did not include zero. By Phase 2, approximately 12 years post-thinning, the difference in mean observation rates between the HT and CO was statistically non-significant (for Steller’s Jay: p-value = 0.83, Tukey-adjusted lsmeans; Fig. 2; for Canada Jay: p-value = 0.99, Tukey-adjusted lsmeans, Fig. 3). Our data did not show a statistically significant effect of thinning on corvid activity in the LT treatment throughout the study.

**DISCUSSION**

Our analysis provided evidence that, as expected, presence of avian nest predators can increase in response to thinning in young (< 50-yr-old) Douglas-fir stands. The increase in activity of both Steller’s and Canada Jays immediately after heavy thinning is consistent with previous findings of positive response of both species to forest management practices that create edge and contribute to landscape patchiness (Waterhouse and Armleder 2007, Walker et al. 2020). Thinning caused structural changes such as reduced canopy cover within the stands, and edges along stand perimeters and around canopy gaps within the LG treatment, with which jays and other corvid nest predators have been positively associated (Andren 1992, Ibarzabal and Desrochers 2004, Marzluff et al. 2004). Jays in our study may have been responding to increased food availability associated with these structural changes. Increases in densities of open-cup nesting songbirds in response to thinning have been documented on the same study sites (Hagar et al. 2004), and within the Marbled Murrelet nesting zone in the Oregon Coast Ranges (Hayes et al. 2003, Cahall et al. 2013). The combination of these increases in a potential prey resource and canopy openings that can facilitate predator access to songbird nests (Chambers 1996) likely created favorable foraging conditions for avian nest predators. In addition, reduction in overstory density through thinning can promote productivity of fruit-bearing shrubs (Wender et al. 2004), thus increasing availability of another food resource for jays (Marzluff and Neatherlin 2006, Walker et al. 2020).

Density and pattern of residual trees following thinning influenced the magnitude of the response of jays for up to 7 years post-thinning. Initial canopy reduction of > 50% in the HT and LG treatments was sufficient to result in differences in canopy cover between these treatments and the CO that persisted for at least 5 years after thinning (Davis et al. 2007). In contrast, a lack of detectable response in the LT treatment likely reflected the minimal reduction of canopy cover, which was so slight (average canopy cover reduction of < 30%) that no difference from unthinned CO stands was detectable by 3 years after thinning (Davis et al. 2007).

Notwithstanding the initial substantial reduction in canopy cover in the HT treatment, the effect of heavy thinning on jay activity was no longer detectable 12 years later. Simplified crown structure and uniform canopy cover created by removal of many of the suppressed and intermediate trees (Smith et al. 1997), and even spacing of residual trees in the HT treatment reduced spatial heterogeneity in the overstory (Bailey and Tappeiner 1998). Therefore, the ephemeral effect of thinning on jay activity likely reflected the attainment of canopy closure in the heavily thinned stands that was functionally similar to that in unthinned stands after a little over a decade of canopy expansion. This hypothesis is consistent with the suggestion by Marzluff et al. (2000) that maturing, simple-structured forests might provide buffers around old-growth stands used by murrelets for nesting because they harbor relatively few predators.
The slight evidence we found of an increase in Steller’s Jay activity in the LG treatment in the first years following thinning (Fig. 2) justifies caution in the application of thinning-with-gaps where protection of Marbled Murrelet nesting habitat is a goal. The canopy gaps in the LG treatment resulted in the greatest amount of “hard” edge (Malt and Lank 2007) because they were essentially small, clear-cut patches. Documenting overstory response to thinning in the same experimental units we evaluated, Davis et al. (2007) found that hard edges around canopy gaps persisted longer than the “soft edges” defining perimeters of all thinned stands, creating the potential for a prolonged effect on jay activity (Brand and George 2001). Minimizing forest edges with distinct contrast in tree height or density may be key to reducing threat of corvid nest predation for vulnerable species such as the murrelet (Hamer and Nelson 1995, Malt and Lank 2007, 2009). Additional research to further investigate the effects of variation in gap size and density in this type of treatment could help clarify the magnitude and duration of nest predator response.

Our finding of an increase in the activity of two regionally important avian nest predators in response to thinning highlights the importance of careful consideration of the trade-offs involved with the use of thinning as a tool for restoring murrelet nesting habitat. Considering the previously documented positive correlation between jay abundance and risk of nest predation (Luginbuhl et al. 2001, Vigallon and Marzluff 2005), our results suggest that thinning that reduces canopy cover by more than 30% adjacent to murrelet nest stands could result in a short-term increase in risk of nest predation because corvid nest predators are known to expand foraging into vegetation adjacent to disturbed habitat (Andren 1992, Malt and Lank 2009). Furthermore, when stand density reduction is sufficient to significantly increase tree growth, the elevated risk of nest predation may persist for at least 7 years after thinning. Although light thinning (< 30% canopy removal) is less likely to increase corvid activity, it is also less effective for accelerating tree growth and hastening development of old-growth forest structure (Davis et al. 2007). Conversely, more intensive thinning, and variable density thinning that includes canopy gaps, is likely to be most effective for promoting development of mature forest structure (Carey 2003, Puettmann et al. 2016). Variable density thinning prescriptions, like the LG treatment in our study, are currently recommended and widely applied within management agencies to promote diversity in young managed forests (USDA 2020). Therefore, where restoring nesting habitat for the Marbled Murrelet is a goal, the short-term risk of increased nest predation needs to be balanced against the greater potential of intensive thinning to expedite development of old-forest structure.
CONCLUSION
Thinning is an important tool for restoring diversity in forest stands with a legacy of simplified structure from decades of intensive management for timber production. However, the ephemeral negative effects of intensive thinning for some species merit a strategic application that maintains landscape-level connectivity through time. Incorporating our quantitative information on the duration of the effects of thinning into landscape-level planning can help managers balance short- and long-term goals for conservation of species associated with mature, closed-canopy forests. Our results suggest that the application of heavy or variable density thinning as a restoration tool could be cautiously applied in areas that contribute to expansion and connectivity of mature forest reserve networks over the long term, and where risk of short-term degradation of current intact late-seral forest is low. For example, as previously recommended by Malt and Lank (2009), retention of buffers of closed-canopy (unthinned) young forest around stands suitable for murrelet nesting may be a prudent strategy to minimize risk of nest predation. Therefore, to minimize the risk of nest predation associated with increased jay abundance, we recommend retaining unthinned buffers between currently reserved older forest and restoration projects that use intensive thinning to promote development of future mature forest habitat.

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Data Availability:
https://www.sciencebase.gov/catalog/item/618c4cf9d34ec04fc9c863e7.

LITERATURE CITED


Perisoreus canadensis


http://www.ace-eco.org/vol19/iss1/art3/


Appendix 1. Avian species used in an occupancy model to test for community-level differences in detectability between thinning treatments and no-thin controls, before and after implementation of thinning, in a long-term silvicultural experiment, the Young Stand Thinning and Diversity Study, 1992–2007, Oregon Cascade Ranges, USA.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
</tr>
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<tbody>
<tr>
<td>Black-throated gray warbler</td>
<td><em>Setophaga nigrescens</em></td>
</tr>
<tr>
<td>Black-headed grosbeak</td>
<td><em>Pheucticus melanocephalus</em></td>
</tr>
<tr>
<td>Chestnut-backed chickadee</td>
<td><em>Poecile rufescens</em></td>
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<tr>
<td>Dark-eyed junco</td>
<td><em>Junco hyemalis</em></td>
</tr>
<tr>
<td>Golden-crowned kinglet</td>
<td><em>Regulus satrapa</em></td>
</tr>
<tr>
<td>Hammond’s flycatcher</td>
<td><em>Empidonax hammondii</em></td>
</tr>
<tr>
<td>Hermit thrush</td>
<td><em>Catharus guttatus</em></td>
</tr>
<tr>
<td>Hermit warbler</td>
<td><em>Setophaga occidentalis</em></td>
</tr>
<tr>
<td>Hutton’s vireo</td>
<td><em>Vireo huttoni</em></td>
</tr>
<tr>
<td>MacGillivray’s warbler</td>
<td><em>Geothlypis tolmiei</em></td>
</tr>
<tr>
<td>Pacific-slope flycatcher</td>
<td><em>Empidonax difficilis</em></td>
</tr>
<tr>
<td>Red-breasted nuthatch</td>
<td><em>Sitta canadensis</em></td>
</tr>
<tr>
<td>Swainson’s thrush</td>
<td><em>Catharus ustulatus</em></td>
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<tr>
<td>Varied thrush</td>
<td><em>Ixoreus naevius</em></td>
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<tr>
<td>Townsend’s solitaire</td>
<td><em>Myadestes townsendi</em></td>
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<tr>
<td>Warbling vireo</td>
<td><em>Vireo gilvus</em></td>
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<tr>
<td>Western tanager</td>
<td><em>Piranga ludoviciana</em></td>
</tr>
<tr>
<td>Pacific wren</td>
<td><em>Troglodytes pacificus</em></td>
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