

IMPACTS OF STRUCTURE RETENTION ON AVIAN ECOLOGY IN MANAGED FORESTS OF
THE PACIFIC NORTHWEST

By

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ABSTRACT

IMPACTS OF STRUCTURE RETENTION ON AVIAN ECOLOGY IN MANAGED FORESTS OF THE PACIFIC NORTHWEST

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Structure retention is a practice used in managed forests to assist the conservation of biological diversity, whereby green trees, dead trees (i.e., snags), and downed wood are retained during timber harvest. This activity is recognized as beneficial; however, there is little scientific support to guide the management prescriptions (e.g., density, patch sizes, distribution pattern). I quantified wildlife responses to structure retention attributes in harvest units across 4 regions in the Pacific Northwest, USA, during the summers of 2008–2010. These 4 regions encapsulated ecological and management variability of intensively managed forests ranging from Washington to northern California. Bird species were observed at retention sites across the 4 regions and white-headed woodpeckers (*Picoides albolarvatus*) were studied more intensively in California. I used a hierarchical modeling framework to separately model the processes related to data collection (e.g., detection probability) from those related to the state variables of interest (e.g., species occupancy). This framework allowed for the examination of factors which influenced each process. The results provide empirical support for management strategies that can improve the effectiveness of structure retention for addressing biodiversity objectives.

In the first chapter, I report on a multi-species occurrence model which estimated occupancy and detection probabilities for all bird species observed at retention sites. Retained tree count was associated with an increased occupancy probability for 70% of the observed species. The community response to tree count was consistent across all study

areas and years – species richness estimates increased with tree count and approximated a species-area curve. Distance to nearest mature forest did not significantly affect occupancy probability for any observed species, and therefore, had no significant relationship with species richness. These results suggest that the diversity of birds using structure retention in harvest units can be maximized at patches of >10–15 rotation age trees.

In the second chapter, I used a multistate site occupancy model to estimate the probabilities of occupancy and nesting for white-headed woodpeckers in harvest units where structure retention was present. Snag density had a significant positive association with nesting probability. Mature forest proportion was negatively associated with nesting probability, though there was considerable uncertainty. High occupancy (0.98) and nesting (0.89) probabilities suggest that current structure retention policies have provided the necessary habitat conditions for white-headed woodpecker nesting in harvest units of northern California. Forest managers can maximize nesting probability by retaining >2 snags/ha during harvest.

In the third chapter, I examined reproductive success for white-headed woodpeckers using models of nest survival and number of young fledged. We documented a high nest success rate (0.85) and found that successful nests were most likely to produce ≥ 3 young. None of the habitat variables that were examined at multiple scales were able to significantly describe variation in either metric of reproductive success. Current forest management practices in northern California appear to be providing habitat conditions that are conducive to the species' persistence in this region.

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INTRODUCTION

Loss of biodiversity caused by human activities is recognized as a major threat to ecological communities across the planet (Wilson, 1999). This threat is related not only to ethical and aesthetic values, but also goods and services derived from diverse ecosystem properties (Hooper *et al.*, 2005). Biodiversity is hypothesized to serve as insurance that counteracts environmental fluctuations which could otherwise severely alter the properties of ecosystems (Folke *et al.*, 1996; Naeem and Li, 1997). The underlying premise is that communities with greater biodiversity are more resilient to environmental disturbances. As such, the development of policies that incorporate the maintenance of biodiversity into resource management has become more widespread (Redford and Richter, 1999).

Biodiversity is often used synonymously with species richness, though the former incorporates more than simply taxonomic diversity. The concept of biodiversity refers to the diversity of living organisms and their interactions with the environment that exist within and across all scales—spatial, temporal, and biotic—of ecological organization (Noss, 1990; Angermeier and Karr, 1994; Hooper *et al.*, 2005). The complexity of this definition is difficult for humans to comprehend thereby exacerbating problems already associated with effective resource management when sustaining biodiversity becomes the conservation goal (Bunnell and Huggard, 1999). The species pool within a community is often used as a surrogate for biodiversity because it represents an entity that is easy to measure and understand (Bunnell and Huggard, 1999). Using taxonomic diversity alone may not be effective for quantifying biodiversity, as species typically do not have equal

impacts on the processes within an ecosystem due to differences in their functional traits (Chapin *et al.*, 2000; Hooper *et al.*, 2005). Functional diversity attempts to address both species and ecological processes (Petchey and Gaston, 2002).

A reduction in ecosystem functions is hypothesized to parallel a reduction in biodiversity for a given community, though this relationship is complex and at times ambiguous (Loreau *et al.*, 2001). There are still many unanswered questions regarding the effects of biodiversity on ecosystem productivity and stability, and the efficiency of resource use by organisms; the context dependency of these relationships makes the formulation of consistent ecological models difficult (Naeem, 2002). It can be postulated that since species must be occupying fundamentally different niche spaces to coexist within a given community, any loss of species will result in a loss of ecosystem function; the magnitude and significance of this loss are proportional to the difference in functional traits between the lost species and its neighbors (Lawton *et al.*, 1998). Functional traits that are unique and possessed by only a few species present the greatest threat of lost ecosystem function when biodiversity is reduced (Marcot and Vander Hayden, 2001). Communities with a high level of functional redundancy among species, which is usually correlated with high biodiversity, are more resilient to changes in environmental conditions (Naeem, 1998; Marcot and Vander Hayden, 2001).

Keystone species typically occupy a unique niche space with little redundancy, resulting in their relatively disproportionate influence on the ecosystem (Power *et al.*, 1996). Especially important are keystone species that act as ecosystem engineers, which according to Lawton and Jones (1995:142), “directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in

biotic or abiotic materials.” While single species management is generally criticized for being one-dimensional, the importance of keystone species is explicit and represents a unification of ecosystem management practices for the conservation of biodiversity (Simberloff, 1998; Callicott *et al.*, 1999).

Despite the uncertainty in its utility and meaning, the maintenance of biodiversity has become a goal for forest management (Bunnell and Johnson, 1998). Forest management evolved during the last century from a focus on the extraction of valuable commodities to one that recognized multiple interests and sought to maintain the essential elements of forest ecosystems. Aubry (2007) summarized the history of this evolution in the Pacific Northwest region of the USA, where an increased understanding of forest ecology and relationships between vertebrate species and unique structural elements of vegetation communities (e.g., riparian and old-growth forests) led to the enactment of multiple environmental laws and major policy changes for public lands during the 1980s. The concept of a “new forestry” was proposed as a means to balance the conflicting goals of timber extraction and biodiversity conservation (Franklin, 1989). Among the components of new forestry was legacy retention, a stand-scale silvicultural practice whereby legacies of the original stand (e.g., large live and dead trees, and other structural habitat elements) are retained during harvest (Franklin, 1989). Cavity-nesting species require dead trees (i.e., snags) for nest sites, and some primary cavity excavators act as keystone species and ecosystem engineers by creating cavities for other species (Aubry and Raley, 2002; Bednarz *et al.*, 2004; Martin *et al.*, 2004). Structure retention would, therefore, provide a structural diversity more similar to that of naturally disturbed forests than would traditional clearcutting. This practice could potentially facilitate a wider range of ecological

functions and species and, thus, promote biodiversity (Hansen *et al.*, 1995; Franklin *et al.*, 2002).

Implementation of structure retention practices are mandated for both public and private nonfederal forests in the Pacific Northwest by state forest practices rules (Washington Forest Practices Board, 2002; Oregon Department of Forestry, 2005; California Department of Forestry and Fire Protection, 2007). These rules attempt to reduce the impacts of timber harvesting on ecosystem properties (both biotic and abiotic) through operational guidelines related to harvesting and replanting activities (e.g., road construction on steep slopes and proximity to wetlands). Retention of structural features is incorporated into forest practices rules by restricting harvest within riparian zones and requiring minimum densities of standing live and dead trees and down logs (each with minimum size dimensions) within harvest units. Some private landowners also participate in forest stewardship programs that may require additional structural retention measures to meet a third-party certification. For example, as of 2011 the Sustainable Forestry Initiative enrolled 74 million ha of forestlands in North America (Sustainable Forestry Initiative, 2011). The certification standard includes an indicator specifically pertaining to retained structures. While these management efforts are likely beneficial, it is unclear how specific properties of retained structures (e.g., spatial distribution, density, size) actually influence biodiversity (Franklin *et al.*, 2002).

Our goal was to quantify the contribution of retained structures for providing wildlife habitat and influencing biodiversity within managed forests. The National Council for Air and Stream Improvement (NCASI) recently identified the need for research to evaluate the effectiveness of structure retention policies, including their contribution to

wildlife diversity and their role in providing habitat for cavity-nesting species (NCASI, 2008). We quantified the physical attributes of retained structures and examined relationships between structure attributes and wildlife use, with special emphasis on cavity-nesting birds. We focused on retained structures that were specifically preserved during harvesting to meet or exceed regulations set by state forest practices rules, including large green trees, dead trees (or snags), and patches of these elements. Results of the study are presented in 3 separate chapters. The first chapter examines use of retained structures by the entire bird community to understand how structure attributes influence species richness across 4 regions of the Pacific Northwest ranging from Washington to northern California. The second and third chapters focus on white-headed woodpecker (*Picoides albolarvatus*) ecology in harvest units of northern California. White-headed woodpeckers may serve as a keystone species in dry forests of western North America where they are abundant, given their role as primary excavators. The analyses examine how habitat attributes at multiple scales influence stand-level nesting probability (chapter 2) and reproductive success (chapter 3) for white-headed woodpeckers. Each chapter concludes with a discussion of management implications.

CHAPTER 1

CONSERVING AVIAN RICHNESS THROUGH STRUCTURE RETENTION
IN MANAGED FORESTS OF THE PACIFIC NORTHWEST

Abstract

Structure retention is a practice used in managed forests to assist the conservation of biological diversity, whereby green trees, dead trees (i.e., snags), and downed wood are retained during timber harvest. This activity is recognized as beneficial; however, there is little scientific support to guide the management prescriptions (e.g., patch sizes, distribution pattern). We quantified the response of birds to structure retention in timber harvest areas located in the Pacific Northwest. We used a hierarchical community model to examine how size (tree count) and location (distance to forest edge) of retention sites influenced the species richness of birds using sites. The modeling framework integrated multiple species-specific occupancy models that accounted for imperfect detection to produce estimates of species richness. We sampled a biogeoclimatic gradient by selecting harvest units within four separate regions (two in Washington, one each in Oregon and California) that support different forest types. Observations were conducted at a random selection of retention sites (e.g., patches, individual trees) within harvest units to record bird use in the breeding seasons of 2008 and 2009. Estimated occupancy and detection probabilities differed by species and region. Retained tree count was associated with an increased occupancy probability for 70% of the observed species, including both forest-dependent and open/generalist birds. The community response to tree count was consistent across all study areas and years – species richness estimates increased with tree

count and approximated a species-area curve. Edge distance did not significantly affect occupancy probability for any observed species, and therefore, had no significant relationship with species richness. These results suggest that the diversity of birds using structure retention in harvest units can be maximized at patches of >10–15 rotation age trees. Forest managers are encouraged to group green-trees around high-quality snags and other unique wildlife trees where possible, and to vary prescriptions across stands to provide habitat heterogeneity at the landscape scale.

Keywords: avian richness, forest practices rules, hierarchical community modeling, managed forests, occupancy, Pacific Northwest, structure retention

1. Introduction

Conservation of biological diversity is a consideration during forest management (Lindenmayer and Franklin, 2002). The effectiveness of structure retention as a means to conserve biological diversity within intensively managed forests is poorly understood (NCASI, 2008). Structure retention is a management practice whereby green trees, dead trees (i.e., snags), and downed wood are retained during timber harvest. Structure retention provides residual habitat elements of mature forests that might otherwise be lost during timber harvesting and forest regeneration activities; these habitat elements are critical resources for numerous forest-dwelling wildlife (Thomas *et al.*, 1979; Swanson and Franklin, 1992; Bull *et al.*, 1997; Hunter and Bond, 2001; Rosenvald and Löhmus, 2008). For example, Rose *et al.* (2001) suggested that 93 wildlife species have habitat requirements associated with snags in Washington and Oregon, including 63 species of birds that use snags for nesting (i.e., in cavities) or foraging.

Whether structure retention ultimately impacts biological diversity depends on how resultant patterns of habitat complexity and the amounts of critical resources (like snags) meet the requirements of individual wildlife species at relevant scales. Thus, the difficulty of managing for biodiversity (i.e., accommodating the requirements of many species) becomes apparent (Bunnell and Johnson, 1998). Structure retention is currently regulated at the stand-level on state and private lands in the Pacific Northwest (Washington, Oregon, and California) by state forest practices rules, which include criteria for retaining minimum densities and diameters of green trees, snags and downed logs during forest management activities (Washington Forest Practices Board, 2002; Oregon Department of Forestry, 2005; California Department of Forestry and Fire Protection,

2007). Additionally, forest practices rules regulate activities in and around riparian management zones and other sensitive areas (e.g., unstable slopes). These rules were developed to balance timber management objectives with the broader conservation needs of the forested landscape.

The forest practices rules pertaining to structure retention were developed to help alleviate the potential negative impacts of even-aged forest management on snags and snag-dependent wildlife species (NCASI, 2008). Diameter retention rules (e.g., minimum tree diameter >25cm) are based on the requirement by cavity-nesting species for decaying trees and snags that are sufficiently large (Thomas *et al.*, 1979; Zarnowitz and Manuwal, 1985; Bull *et al.*, 1997). Density retention rules (e.g., ≥ 10 trees/ha) are intended to ensure that current and future snag resources are not limiting to wildlife species (Neitro *et al.*, 1985; Bunnell *et al.*, 2002). Green-tree retention is intended to serve as the source of future snags, but it may also influence stand-level occurrence of some wildlife species depending on the density and pattern of green trees in the harvest unit (Chambers *et al.*, 1999; Schieck and Hobson, 2000; Bunnell *et al.*, 2002; Walter and Maguire, 2005; Preston and Harestad, 2007). In some states, forest practices rules require a specific distribution of structure retention (e.g., Washington mandates a maximum distance of ~240m between any given point and a retained tree in the harvest unit), though little empirical evidence exists to support such rules. Other states allow forest managers more flexibility in deciding on the pattern (i.e., clumped or dispersed) and location of structures. Forest managers can maximize the utility of retained structures as a habitat resource by implementing retention patterns with the greatest positive impact on the wildlife community.

Evaluation of management actions requires that the biologically relevant quantity of interest (i.e., state variable) be properly defined for monitoring (Yoccoz *et al.*, 2001), and species richness is a common choice for state variable in the context of biodiversity conservation. Species richness can be problematic as a management target because heterogeneity in species detectability can invalidate naïve estimates of species richness (Boulinier *et al.*, 1998). Additionally, species typically do not equitably impact processes within an ecosystem due to differences in their functional traits (Chapin *et al.*, 2000; Hooper *et al.*, 2005). Hence the interpretation of species richness without some consideration of species detectability and identity can be misleading. A hierarchical modeling framework that incorporates imperfect species detection during sampling and generates species-specific detection and occupancy (proportion of sites occupied) probabilities can be used to produce valid estimates of species richness (Dorazio *et al.*, 2006; Kery and Royle, 2008; Royle and Dorazio, 2008). This type of multi-species occupancy model has been used to evaluate the effects of management actions and landscape changes on species richness for entire avian communities and subsets of functionally similar species that may have different responses to specific habitat alterations (e.g., Ruiz-Gutierrez *et al.*, 2010; Zipkin *et al.*, 2010).

Our study used a hierarchical multispecies occupancy model to understand how attributes of structure retention sites in timber harvest units affect avian species richness within private industrial forests of the Pacific Northwest. Retention sites, hereafter, refer to single trees or patches of multiple trees that are left standing during harvesting operations to meet or exceed the requirements mandated by state forest practices rules. We focused on two attributes of retention sites that can be easily modified during

harvesting operations and likely impact occupancy by individual bird species: 1) number of trees retained (i.e., tree count); and 2) location within the harvest unit (i.e., distance to forest edge). In addition to total species richness, we estimated the richness of a functional group that forages or nests (or both) in the forest canopy and would presumably be absent from recently harvested forests that lack structure retention. Given that structure retention is intended to help conserve biological diversity, the response by species that are typically negatively affected by timber harvest should be a priority for evaluating the effectiveness of structure retention practices.

2. Methods

2.1. Study areas

Our study was conducted in 4 separate areas in the Pacific Northwest (Washington, Oregon, and California) that spanned multiple biogeoclimatic regions (i.e., sections, sensu Bailey, 1988), including the Northern Cascades, Oregon and Washington Coast Ranges, and the Southern Cascades (Figure 1.1). We refer to each study area by the general location in the state within which it occurred: central Washington (CWA), southwest Washington (SWA), southwest Oregon (SOR), and northern California (NCA). All study areas were located within forested watersheds on private industrial ownership with a long history of management (second and third rotation stands). Watersheds contained a heterogeneous matrix of stand age classes and some had mixed ownership (e.g., the NCA study area was juxtaposed with the Shasta-Trinity National Forest). We identified all harvest units that had been logged 3–12 years prior using a geographic information system (GIS). For each study area, we calculated summary statistics on stand area and elevation and randomly

selected ~20 harvest units that represented average conditions available on the landscape (i.e., area and elevation values were <1 standard deviation from the study area mean). In total, we selected 84 harvest units that fell into 2 general area classes, small (4–12ha) and large (22–61ha), and ranged from 20–1830m in elevation, and from 41.1–47.7° latitude (Table 1.1).

2.2. Retention site selection and measurement

We examined the harvest units in each study area to identify retention sites that could be selected for sampling using 1-m resolution aerial photography collected from the National Agriculture Imagery Program (NAIP; <http://www.apfo.usda.gov/>) during 2005–2006. We field-verified all photo-identified retention sites during reconnaissance surveys in 2006. Reconnaissance surveys included a thorough census of each harvest unit to identify additional retention sites not visible from the imagery (e.g., individual snags). We delineated retention sites in the field based on the felling distance of trees at and around the site. For example, an individual tree was considered a distinct retention site only if the distance to the nearest adjacent tree was greater than the height of either tree. GPS coordinates were recorded at the center of each retention site and edge distance was calculated in a GIS to the nearest mature forest (>40 years old) as determined by interpretation of the NAIP imagery. We used a stratified random selection to identify retention sites for further sampling in each study area. Stratification was necessary to ensure that retention sites with a range of tree counts were selected given the prevalence of retention sites with tree count = 1. The strata were defined by the tree count at each retention site and consisted of 4 groups: 1 tree, 2–5 trees, 6–15 trees, and >16 trees. Selected retention sites located within the same harvest unit were required to be >150 m

apart to decrease spatial dependence, resulting in 1–9 sites per harvest unit depending on the area and shape of the unit. For each selected retention site, we used variable radius plots to tally and measure trees >12.7cm diameter at breast height (dbh) with a basal area factor 10 prism.

2.3. Bird surveys

We observed birds using retention sites during the breeding season (May–July) at 241 sites in 2008 and 203 sites in 2009; 95 sites were surveyed in both years, resulting in 349 unique retention sites over the duration of the study. Each survey consisted of 2 observers recording all birds that interacted with a retention site (e.g., perched on a branch, foraged on a trunk) for a duration of 30min starting at a randomly selected time between sunrise and 5 hours later. Observers were located >25m to the east of the retention site to avoid disturbance and obtain the best lighting for visual detection; surveys began after a 2-min settling period upon arrival. Observers recorded the species, location (e.g., trunk, branch), and behavior (e.g., perching, foraging) of all individuals detected at a retention site, in addition to the times (recorded to the nearest second) at which the individual arrived and departed. Both observers made an effort to detect birds visually and aurally, though one observer was primarily responsible for recording while the other focused solely on viewing the retention; these duties were alternated. Surveys were conducted during adequate wind (<12km/h) and weather (no rain or fog) conditions (Ralph *et al.*, 1995). We trained observers for 2 weeks prior to sampling with portable media players to improve their abilities in identifying bird species by sight and sound.

2.4. Modeling framework

We used the hierarchical modeling framework described in Royle and Dorazio (2008) that has been developed and applied in other studies (e.g., Dorazio *et al.*, 2006; Kery and Royle, 2008; Dorazio *et al.*, 2010; Ruiz-Gutierrez *et al.*, 2010; Zipkin *et al.*, 2010). The framework uses a state-space formulation that separates the ecological process (true occurrence for a given species, which is unobserved) from the observation process (detection of species presence); observations or detections are modeled conditional on the latent process of occurrence (Royle and Kery, 2007). This separation allows for proper partitioning of uncertainty and examination of covariates that are distinctive to each process. The multispecies model estimates species-specific occupancy and detection probabilities which can be combined to calculate community-level metrics such as the species richness of a site while accounting for species that were never observed. A major benefit of the multispecies approach is that the species-specific model parameters are all treated as random effects governed by a common community-level distribution, resulting in a more parsimonious model with greater precision for parameter estimates, especially for rare species (Royle and Dorazio, 2008). The precision of parameter estimates is improved for any species with sparse detection data because the estimates for each individual species are informed by the data across all species (Dorazio *et al.*, 2010). The approach is more efficient than estimating fixed parameters separately for each species in a large multispecies dataset, which would be limited to species having an adequate number of detections (Royle and Dorazio, 2008).

To create the repeated measures design necessary for estimating occupancy and detection probabilities (MacKenzie *et al.*, 2002), we divided each 30 minute bird survey

into three 10-min intervals. Following MacKenzie and Royle (2005), we interpreted occupancy as “use” given that the closure assumption was not valid – we assumed most bird species had territories that were larger than retention sites and, therefore, would be periodically unavailable for detection during surveys. We also assumed that detection was primarily a function of that availability (i.e., the probability that a species is available for detection, given that it is present at a site) and not a function of imperfect detection by the observers. We were confident that 2 observers could adequately detect all species that were present at a retention site during a survey, given the clear path of sight and small viewing window necessary to observe sites. To account for the potential lack of independence among observation intervals, we estimated detection probabilities for intervals with previous detections separately from intervals with no previous detections (Mordecai *et al.*, 2011).

We constructed a detection history for each species i at retention site j which indicated for each survey interval k in year t whether a species was detected ($y = 1$) or undetected ($y = 0$). Our model notation is consistent with the state-space formulation presented by Royle and Kery (2007) for modeling occupancy and detection probabilities. For a species to be detected during a survey interval, the species had to be periodically present at the retention site during a given year; therefore, the detections y_{ijkt} were conditional on the unobserved occupancy state z_{ijt} such that $y_{ijkt} \sim \text{Bernoulli}(z_{ijt}p_{ijkt})$ where p_{ijkt} is the probability that species i is detected at retention site j during interval k in year t , given that species i is actually present at retention site j in year t . If species i is not present at retention site j in year t then $z_{ijt} = 0$ and $y_{ijkt} = 0$ with a probability of 1.

Note that it is possible to observe a detection history where $y_{ijt} = (0, 0, 0)$ even when $z_{ijt} = 1$ in situations where the species is never detected at the retention site during the survey that year even though it is actually present at some point. We modeled the unobserved occupancy state z_{ijt} such that $z_{ijt} \sim \text{Bernoulli}(\psi_{ijt})$ where ψ_{ijt} represents the probability that species i is present at retention site j in year t .

We built logit-linear models for the probabilities of detection (p_{ijkt}) and occupancy (ψ_{ijt}) to incorporate the effects of covariates for each process. The logit transformation is necessary to allow predicted values in the linear models to range across all real numbers while constraining the back-transformed probabilities to be between 0 and 1. We assumed that species-specific detection and occupancy probabilities were also specific to an individual study area h , and likely varied across years. In the model for detection, we included survey date as a potential covariate with both linear and quadratic terms to accommodate peaks of availability that may occur at any point during the season (Royle and Dorazio, 2008). We also included a binary variable to indicate whether a species had been detected in a previous survey interval (Mordecai *et al.*, 2011). We defined the model of detection as:

$$\text{logit}(p_{ijkt}) = v_{iht} + \alpha_{1i} \text{date}_{jt} + \alpha_{2i} \text{date}_{jt}^2 + \alpha_{3i} \text{Prev}_{ijkt}$$

where v_{iht} is the mean logit-scale detection probability for species i in study area h during year t ; α_{1i} and α_{2i} are the regression parameters for the linear and quadratic effects of survey date; and α_{3i} is the regression parameter estimating the effect of a previous detection, Prev_{ijkt} .

We estimated occupancy separately for each year with a multi-season model which had an initial occupancy probability in year 1 (ψ_{ij1}) followed by a subsequent occupancy probability in year 2 (ψ_{ij2}). Occupancy in year 2 was dependent on the unobserved occupancy state in year 1 (z_{ij1}) and a function of either survival (presence at a retention site in year 2 given presence in year 1) or colonization (presence at a retention site in year 2 given absence in year 1). The models of occupancy for each year incorporated the two site covariates of management interest, number of trees and edge distance, with both linear and quadratic terms. The number of trees was restricted to stems >25cm diameter given that this was the minimum diameter resulting in compliance with the state forest practices rules (NCASI, 2008). We were not interested in modeling occupancy dynamics per se (i.e., effects of covariates on colonization and survival), thus, covariates were assumed to have the same additive effect on occupancy probability for both years. Similar to our detection model, we specified separate mean probabilities for each study area. We defined the occupancy model in year 1 as:

$$\text{logit}(\psi_{ij1}) = u_{ih} + \beta_{1i}trees_j + \beta_{2i}trees_j^2 + \beta_{3i}dist_j + \beta_{4i}dist_j^2$$

where u_{ih} is the mean logit-scale occupancy probability for species i in study area h during year 1 at mean values for the covariates, and the β_i terms are the regression parameters for the linear and quadratic effects of tree count (β_{1i}, β_{2i}) and edge distance (β_{3i}, β_{4i}) at retention site j . Accordingly, the occupancy model for year 2 was:

$$\text{logit}(\psi_{ij2}) = \phi_{ih}z_{ij1} + \gamma_{ih}(1 - z_{ij1}) + \beta_{1i}trees_j + \beta_{2i}trees_j^2 + \beta_{3i}dist_j + \beta_{4i}dist_j^2$$

where ϕ_{ih} and γ_{ih} are the mean logit-scale probabilities of survival (continued presence at a site) and colonization (new presence at a site), respectively, for species i in study area h at mean values for the covariates. Occupancy probability in year 2 is defined by survival ϕ_{ih} when $z_{ij1} = 1$ and by colonization γ_{ih} when $z_{ij1} = 0$. The regression parameters for tree count (β_{1i}, β_{2i}) and edge distance (β_{3i}, β_{4i}) are specified the same as in year 1.

As part of the multi-species hierarchical modeling framework, we treated the parameters for occupancy and detection models as random effects with each species-specific parameter being drawn from a common distribution specified by a mean and variance. The mean and variance quantified the community-level responses across species, assuming that the species under consideration were ecologically similar (see below) and the heterogeneity across species could be described by a normal distribution (Kery and Royle, 2008). We specified 2 habitat groups of bird species, forest and open, with separate parameter distributions to account for potential differences in ecological responses to forest management. The forest group represented species that require mature trees to fulfill some life requisites (e.g., cavity/canopy nesters, bark/canopy foragers; Martin, 1995) and could be considered “forest dependent”; the open group represented all other species which were either habitat generalists or were known to prefer relatively open vegetation types (e.g., shrubs, young forest). As an example, we defined the parameter representing the linear effect of tree count on occupancy probability as:

$$\beta_{1i}[\text{FOREST}] \sim N\left(\mu_{\beta_1}[\text{FOREST}], \sigma_{\beta_1}[\text{FOREST}]\right)$$

where $\mu_{\beta_1}[\text{FOREST}]$ is the mean response across forest species and $\sigma_{\beta_1}[\text{FOREST}]$ is the standard deviation. Each parameter in the models for occupancy and detection was

assigned its own hyperparameters (i.e., μ and σ), and the species-specific parameter estimate was drawn from the distribution specified by the hyperparameters.

We calculated site-level richness in each year, N_{jt} , by summing the unobserved occupancy states across species such that $N_{jt} = \sum_{i=1}^n z_{ijt}$ for the $i = 1, \dots, n$ species that were observed. We also calculated the site-level richness for each subset of species in the forest and open groups. We did not use data augmentation to incorporate unobserved species into the estimates of richness, as outlined in Dorazio *et al.* (2006) and illustrated in other applications of hierarchical multispecies models (e.g., Dorazio *et al.*, 2010; Zipkin *et al.*, 2010). Russell *et al.* (2009a) argued that using “unseen, hypothetical species” as a basis for management recommendations to regulatory agencies would be problematic. Our estimates of species richness are still improved over the observed counts for individual sites by accounting for those species that were observed in the study area but never detected at a given sampling site. We examined relationships between site-level richness and the covariates associated with occupancy (edge distance and tree count) while acknowledging that the model does not formally quantify these relationships (see Zipkin *et al.*, 2010). Site-level richness is a derived quantity determined by the collection of species-specific occupancy probabilities for a given retention site, with the unobserved occupancy state being contingent on covariate values. We present the relationships between richness and retention site covariates graphically.

We used a Bayesian analysis to estimate the parameters and calculate community-level summaries with Markov chain Monte Carlo (MCMC) methods in WinBUGS (Spiegelhalter *et al.*, 2003). WinBUGS uses Gibbs sampling (Geman and Geman, 1984) to draw samples of all unknown quantities from the joint probability distributions specified

by the models. In this way, a posterior probability distribution for each parameter is estimated, from which summary statistics such as means and credible intervals (the Bayesian analog to a confidence interval) can be calculated. We operated WinBUGS with program R (R Development Core Team 2011) through the R2WinBUGS package (Sturtz *et al.*, 2005). We chose non-informative prior distributions for all hyperparameters. The prior distribution for each of the mean hyperparameters (μ) was specified as a uniform distribution between 0 and 1 on the probability scale for model intercepts and a diffuse normal distribution with mean = 0 and variance = 1000 for regression coefficients. The prior distribution for each of the standard deviation hyperparameters (σ) was specified in terms of the precision (i.e., inverse variance) using a gamma distribution with shape = 0.1 and scale = 10. All covariate values were standardized to have a mean of 0 and a unit variance of 1. We examined model results based on 3 chains of 75,000 iterations after discarding the first 25,000 iterations and thinning by 50; this process resulted in 3,000 values forming the posterior distribution for each parameter. We determined model convergence by examining trace plots of the posterior distributions for each chain and by assessing the R-hat statistic, or scale reduction factor, which should be <1.1 for all parameters (Gelman *et al.*, 2003). WinBUGS code for model specification is presented in the Appendix (A.1).

3. Results

We observed 47 and 45 bird species using retention sites in 2008 and 2009, respectively, with a total of 54 species across both years. Total detections were relatively low for every species, indicating that birds were rarely observed using retention sites

during the surveys (Table 1.2). Average species-specific detection probabilities reflected the rarity of observations and, along with occupancy probabilities, were variable within and across study areas and years (Figure 1.1). Average species-specific detection probabilities ranged from 0.01–0.07 in CWA, 0.01–0.07 in SWA, 0.04–0.57 in SOR, and 0.01–0.15 in NCA ; average species-specific occupancy probabilities ranged from 0.05–0.63 in CWA, 0.02–0.98 in SWA, 0.02–0.33 in SOR, and 0.14–0.93 in NCA. There were no significant correlations between estimated occupancy and detection probabilities for any of the study areas (Figure 1.2), indicating that the probability of a bird being detected at a retention site (i.e., being present in the part of its territory that overlaps a site) was not significantly related to the probability of the bird ever using the retention site (i.e., having a territory that overlaps a site). Our assessments of model fit indicated that convergence was achieved: R-hat was <1.1 for all model parameters (mean = 1.01) and trace plots suggested adequate mixing.

Covariates affecting occupancy and detection probabilities in the log-linear models differed by species and habitat group in the significance of their regression coefficients (Figures 1.3, 1.4); significance is indicated when the 95% credible interval [CI] does not overlap zero. Detection probabilities were shown to increase with survey date for 4 species including American Robin, Band-tailed Pigeon, Cedar Waxwing, and Dark-eyed Junco (Figure 1.3a). A single species, Hairy Woodpecker, exhibited a significantly negative quadratic relationship between detection probability and survey date (Figure 1.3b), suggesting that detection probability was higher during the middle of the survey season than at either start or end. Detection probability was found to increase significantly in a

given time interval after a detection had occurred in a previous time interval for 8 species (Figure 1.3c).

Occupancy probability for most species (38 of 54; 70%) exhibited a significant positive linear response to tree count; habitat group had a small influence on the distribution or precision of parameters (Figure 1.4a). The 16 species not exhibiting a significant response to tree count included 8 forest species (Black-capped and Chestnut-backed Chickadee, Downy and Hairy Woodpecker, Mountain and Western Bluebirds, Pileated Woodpeckers, Northern Flicker and Tree Swallow) and 8 open/generalist species (American Crow, Bewick's Wren, Lazuli Bunting, Mourning Dove, Rufous Hummingbird, Spotted Towhee, and Townsend's Solitaire). All of the forest species not showing a significant relationship with tree count were cavity-nesters that likely used individual snags more often than green patches. Seven species exhibited a significantly positive quadratic response to tree count including 1 forest species (Western Tanager) and 5 open species (American Robin, Chipping Sparrow, Stellar's Jay, Swainson's Thrush, and White-crowned Sparrow). Edge distance was not a significant predictor of occupancy probability for any species (Figure 1.4c, d).

Mean site-level avian richness was estimated to range from ~1–32 for all species, ~1–12 for forest species, and ~1–22 for open species in both years (Figures 1.5, 1.6). Considering that occupancy probabilities for most species exhibited positive linear responses to tree count (Figure 1.4a), as expected the estimates of site-level richness also increased with tree count in both years for the entire bird community and each habitat group (Figure 1.5). The forms of the relationships between tree count and site-level richness suggested power functions with a maximum richness at around 10–15 trees for all

species and open species, with some differences between study areas (Figure 1.5). Forest species appeared to increase with tree count but the trend was mostly linear without a clear asymptote. The absence of significant responses by species to edge distance (Figure 1.4c) resulted in no apparent relationship between mean site-level richness and edge distance, aside from generally lower ranges of estimates at distances >300m (Figure 1.6).

4. Discussion

The effectiveness of structure retention at meeting wildlife conservation objectives may be enhanced by using specific strategies that influence species use of the resources provided by the management actions. Our model results suggested that tree count had a positive effect on the predicted species richness of birds using retention sites in managed forests of the Pacific Northwest. The relationship between species richness and tree count was similar to a power function, which has often been used to describe species-area relationships (Connor and McCoy 1979). There was little difference between the habitat groups (Figures 1.4, 1.5), indicating that both forest and open/generalist species responded similarly to attributes of structure retention, though forest species richness did not appear to reach a maximum. This may have resulted from many forest species, particularly cavity-nesters, being more influenced by snags than live trees in the harvest units; retention sites with more green trees also tended to have more snags. One interpretation of the open species response is that larger patches of retained trees offer a greater amount and diversity of resources (e.g., food, cover) that are beneficial to numerous different species, regardless of specific habitat preferences. Our habitat grouping distinguished species based on certain life history characteristics (Martin, 1995)

but the simple dichotomy would not preclude some similarities in habitat use, especially for generalist species. Ruiz-Gutierrez *et al.* (2010) cautioned on the use of specialist/generalist classifications using previous literature given that species responses do not always follow preconceived expectations. Our classification of forest and open/generalist species was used to allow the parameter distributions to differ for the species in each group; in the absence of a difference (as dictated by the data), classification ends up having no impact on the model results. As expected, many species in the open group were ubiquitous and regularly observed throughout the harvest units, while forest species were almost exclusively observed at retention sites (D.W. Linden, personal observation). Retention site use for open species may have required a short movement from the early successional habitat within the harvest unit, while for forest species it may have required movement from the adjacent mature forest habitat. In either case, the probability of movement to a retention site was likely influenced by the resources provided by the site, resulting in a similar response to tree count by both habitat groups.

Our conclusions are generally consistent with previous research in western North America. Most studies of green-tree retention effects on the avian community in the Pacific Northwest have focused on stand-level responses of species richness and abundance to varying intensities of harvest, with some combination of unharvested control forests, total-harvest clearcuts, and partial-harvest or variable-retention stands serving as treatment units (Beese and Bryant, 1999; Chambers *et al.*, 1999; Preston and Harestad, 2007). These studies have shown that moderate-intensity harvests typically result in stands with a species composition more similar to unharvested forests than to clearcuts and can actually increase species richness as a response to greater habitat complexity, though forest-

dependent birds often exhibit a decreased abundance. Preston and Harestad (2007) suggested that forest-dependent birds increased their use of retention with increasing patch size ranging from 0.25–2ha, though their design did not allow for formal inferences regarding patch size. In boreal forests of Alberta, large residual patches (>100 trees) supported bird communities that were more similar to old contiguous forests than small patches (≤ 10 trees) immediately following stand-replacing disturbances (i.e., fire or harvest) and those differences gradually decreased with time (15, 30 and 60 years post-disturbance) as regenerating trees formed a closed canopy (Schieck and Hobson, 2000). These studies highlight the importance of green-tree retention for providing habitat to members of the forest bird community.

Edge distance was not a significant predictor of use for any observed species and, thus, appeared to have no influence on species richness at retention sites (Figure 1.6). Richness estimates were generally low at distances >300m, but the low sample size at those distances ($n=7$) precludes robust conclusions. While it is possible that bird species responding negatively to edge distance were never observed using retention sites, the lack of an effect may also be attributed to the limited range of distances observed: distance to adjacent forest was <50m for 50% and <200m for 92% of observed retention sites. The distances we observed may have been too small to limit movement by most bird species, especially given that the edge contrast induced by age and structural differences (i.e., regenerating vs. mature forest) could be relatively benign (Ries *et al.*, 2004). Additionally, the calculation of edge distance did not take into account the presence of additional nearby retention sites which may have diluted real effects. There are few examples in the literature to assist our understanding of territory-scale movements by birds in search of

resources outside the preferred habitat type. Desrochers and Fortin (2000) observed Black-capped Chickadee flocks regularly foraging along forest boundaries at distances up to 100m from the edge in a matrix of forest and agriculture. Fraser and Stutchbury (2004) found that an area-sensitive forest bird was willing to move >1km across extensive areas of non-forest in search of a mate, with no indication that movement was restricted to forest corridors. Given the high dispersal capability of birds, the distances to adjacent forest for retention sites observed in our study were likely too small to affect site use. The absence of large distances to adjacent forest are likely an artifact of existing forest practices rules which contain restrictions on the size and juxtaposition of harvest units.

Our dynamic multi-species hierarchical model enabled an estimation of species-specific habitat use across multiple years while accounting for imperfect detection. Our approach followed a modeling framework (Dorazio and Royle, 2005) that has proven effective for estimating multi-species responses to environmental changes resulting from management practices (Russell *et al.*, 2009a; Zipkin *et al.*, 2010) and landscape-scale forest fragmentation (Zipkin *et al.*, 2009; Ruiz-Gutierrez *et al.*, 2010). The major benefit to this approach stems from the specification of species as a random effect governed by a community-level distribution which allows rarely detected species to be incorporated into estimates of species richness and represents a parsimonious approach to modeling multi-species datasets (Royle and Dorazio, 2008).

Our sampling methodology had several limitations in the context of understanding the benefits of structure retention to avifauna. We interpreted occupancy as use because retention sites were typically smaller than the expected territory sizes of the bird species observed in the harvest units and, thus, availability of birds with territories that overlap

retention sites determined our observed differences in detection. Use was defined as the detection of a species at a retention site, but the ecological values of different detections were not always equal: an individual perching for a short time on the branch of a retained green tree is qualitatively different than an individual foraging on a trunk or using a retained snag for a cavity nest. While we observed the full spectrum of use during the study, the low sample size of detections prevented these distinctions from being made for this analysis.

The covariates included in our analysis, tree count (for stems >25cm) and edge distance, represented two attributes that were hypothesized to affect probability of use and were attributes directly linked to operational management decisions and the forest practices rules. However, tree count and edge distance may not have captured the range of biologically relevant characteristics that influence retention site use. We chose tree count over patch size because we felt that birds would perceive retention sites based on the number of trees serving as substrate for resources as opposed to “habitat islands” with different areas; the two measures (tree count and area) were also highly correlated. Tree count also represented a simplified description of attributes at a retention site. Snags provide a different set of resources than live trees and these differences can positively or negatively impact habitat use by a species depending on life history requirements (Thomas *et al.*, 1979; Bull *et al.*, 1997); the same is true for snags with differences in decay state, tree species, or size (Bull, 2002). Unfortunately, the opportunistic nature of snag retention in harvest units made it difficult to sample a wide enough range of snag attributes to examine their effects on retention site use. Snag retention is one of the most difficult management

objectives for industrial forests given that snags have limited lifespans (i.e., amount of time standing) and that snag creation is naturally a highly stochastic process (NCASI, 2008).

5. Management implications

Most bird species using retention sites in harvest units of the Pacific Northwest appear to respond positively to the number of trees retained and, therefore, forest managers can increase the utility of structure retention to avifauna by strategically grouping trees to maximize species richness. We contend a minimum group size for green tree retention of >10–15 trees (with diameters >25cm) is a valid management target for managed forests of the Pacific Northwest that will influence avian species diversity in harvest units. Retention sites with 10–15 large trees will typically range in area from approximately 0.01–0.02ha depending on the target planting density (e.g., 900 trees/ha in Snoqualmie, WA; T. McBride, Hancock Forest Management, personal communication). Our observations suggest that single green trees are rarely used compared to larger patches and given the risk of blowdown, are not useful for meeting tree and snag retention objectives. Given that snag retention is often opportunistic, centering green-tree retention groups around high-quality snags (Bull, 2002) could serve to guide the placement of retention sites. Regardless of the plans for green trees, retention should not be abandoned for single snags or unique wildlife trees that cannot be grouped for operational reasons; these resources should always be left in the harvest unit where possible. While the current study was not able to assess stand-level differences in structure retention, it is understood that forest management prescriptions which are applied similarly across local scales (i.e., stands) can reduce habitat heterogeneity at the larger scale (i.e., landscapes)(Lindenmayer

and Franklin, 2002). Therefore, our management target should not be viewed as an unvarying prescription; rather, varying the group sizes of green-tree retention across harvest units will help create habitat diversity at the landscape scale.

Table 1.1. Attributes of harvest units selected for observing bird use at structure retention sites in managed forests of the Pacific Northwest.

Region ^a	n	Area (ha)			Elevation (m)			Dominant tree species ^b
		Mean	Min	Max	Mean	Min	Max	
CWA	22	8	4	12	350	200	470	WH, DF, RC, Ald
SWA	20	37	24	57	170	20	330	WH, DF, RC, Ald, SS
SOR	20	40	22	61	610	300	800	DF, WH
NCA	23	9	4	11	1500	1250	1830	WF, PP, DF, RF, IC

^a Regions are ordered by latitude, from north to south. Region codes represent the following areas in the Pacific Northwest: CWA = central Washington; SWA = southwest Washington; SOR = southwest Oregon; NCA = northern California.

^b Dominant tree species codes represent the following: Ald = Red alder (*Alnus rubra*); DF = Douglas-fir (*Pseudotsuga menziesii*); IC = California incense-cedar (*Calocedrus decurrens*); PP = ponderosa pine (*Pinus ponderosa*); RC = western redcedar (*Thuja plicata*); RF = red fir (*Abies magnifica*); SS = Sitka spruce (*Picea sitchensis*); WF = white fir (*Abies concolor*); WH = western hemlock (*Tsuga heterophylla*).

Table 1.2. List of species detected using retention sites from 2008–2009 in managed forests of the Pacific Northwest, including habitat group (based on nesting and/or foraging requirements), common name, scientific name, American Ornithologist’s Union alpha code, and total number of detections.

Group	Common name (scientific name)	AOU code	detections
FOREST	Western Tanager (<i>Piranga ludoviciana</i>)	WETA	41
	Mountain Chickadee (<i>Poecile gambeli</i>)	MOCH	40
	Northern Flicker (<i>Colaptes auratus</i>)	NOFL	35
	Yellow-rumped Warbler (<i>Dendroica coronata</i>)	YRWA	30
	Red-breasted Nuthatch (<i>Sitta canadensis</i>)	RBNU	19
	White-headed Woodpecker (<i>Picoides albolarvatus</i>)	WHWO	19
	Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	BHGR	17
	Hairy Woodpecker (<i>Picoides villosus</i>)	HAWO	17
	Red-breasted Sapsucker (<i>Sphyrapicus ruber</i>)	RBSA	12
	Warbling Vireo (<i>Vireo gilvus</i>)	WAVI	12
	Chestnut-backed Chickadee (<i>Poecile rufescens</i>)	CBCH	10
	Tree Swallow (<i>Tachycineta bicolor</i>)	TRES	9
	Mountain Bluebird (<i>Sialia currucoides</i>)	MOBL	6
	Pileated Woodpecker (<i>Dryocopus pileatus</i>)	PIWO	6
	Black-throated Gray Warbler (<i>Dendroica nigrescens</i>)	BTYW	4
	Hutton's Vireo (<i>Vireo huttoni</i>)	HUVI	4
	Violet-green Swallow (<i>Tachycineta thalassina</i>)	VGSW	3
	Western Bluebird (<i>Sialia mexicana</i>)	WEBL	3
	Downy Woodpecker (<i>Picoides pubescens</i>)	DOWO	2
	Townsend's Warbler (<i>Dendroica townsendi</i>)	TOWA	2
	Black-capped Chickadee (<i>Poecile atricapillus</i>)	BCCH	1
OPEN	Dark-eyed Junco (<i>Junco hyemalis</i>)	DEJU	62
	American Robin (<i>Turdus migratorius</i>)	AMRO	30
	Chipping Sparrow (<i>Spizella passerina</i>)	CHSP	27
	Pacific-slope Flycatcher (<i>Empidonax difficilis</i>)	PSFL	26
	Steller's Jay (<i>Cyanocitta stelleri</i>)	STJA	20
	Willow Flycatcher (<i>Empidonax traillii</i>)	WIFL	20
	Band-tailed Pigeon (<i>Columba fasciata</i>)	BTPI	19
	Swainson's Thrush (<i>Catharus ustulatus</i>)	SWTH	18
	Cedar Waxwing (<i>Bombycilla cedrorum</i>)	CEDW	16
	Winter Wren (<i>Troglodytes troglodytes</i>)	WIWR	13
	Dusky Flycatcher (<i>Empidonax oberholseri</i>)	DUFL	12
	Olive-sided Flycatcher (<i>Contopus cooperi</i>)	OSFL	12

Table 1.2 (cont'd)

Wilson's Warbler (<i>Wilsonia pusilla</i>)	WIWA	12
Song Sparrow (<i>Melospiza melodia</i>)	SOSP	9
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	WCSP	9
Rufous Hummingbird (<i>Selasphorus rufus</i>)	RUHU	7
Cassin's Finch (<i>Carpodacus cassinii</i>)	CAFI	6
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	MGWA	6
Spotted Towhee (<i>Pipilo maculatus</i>)	SPTO	6
American Goldfinch (<i>Carduelis tristis</i>)	AMGO	4
Evening Grosbeak (<i>Coccothraustes vespertinus</i>)	EVGR	4
Green-tailed Towhee (<i>Pipilo chlorurus</i>)	GTTO	4
Orange-crowned Warbler (<i>Vermivora celata</i>)	OCWA	4
Purple Finch (<i>Carpodacus purpureus</i>)	PUFI	4
Western Wood-Pewee (<i>Contopus sordidulus</i>)	WEWP	4
Bewick's Wren (<i>Thryomanes bewickii</i>)	BEWR	3
Townsend's Solitaire (<i>Myadestes townsendi</i>)	TOSO	3
Common Raven (<i>Corvus corax</i>)	CORA	2
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	GCKI	2
Lazuli Bunting (<i>Passerina amoena</i>)	LAZB	2
American Crow (<i>Corvus brachyrhynchos</i>)	AMCR	1
Mourning Dove (<i>Zenaida macroura</i>)	MODO	1
Red Crossbill (<i>Loxia curvirostra</i>)	RECR	1

Figure 1.1. Map of study area locations within ecoregions and hydrologic units in the Pacific Northwest, USA. Region codes represent the following areas: CWA = central Washington; SWA = southwest Washington; SOR = southwest Oregon; NCA = northern California.

Figure 1.1 (cont'd)

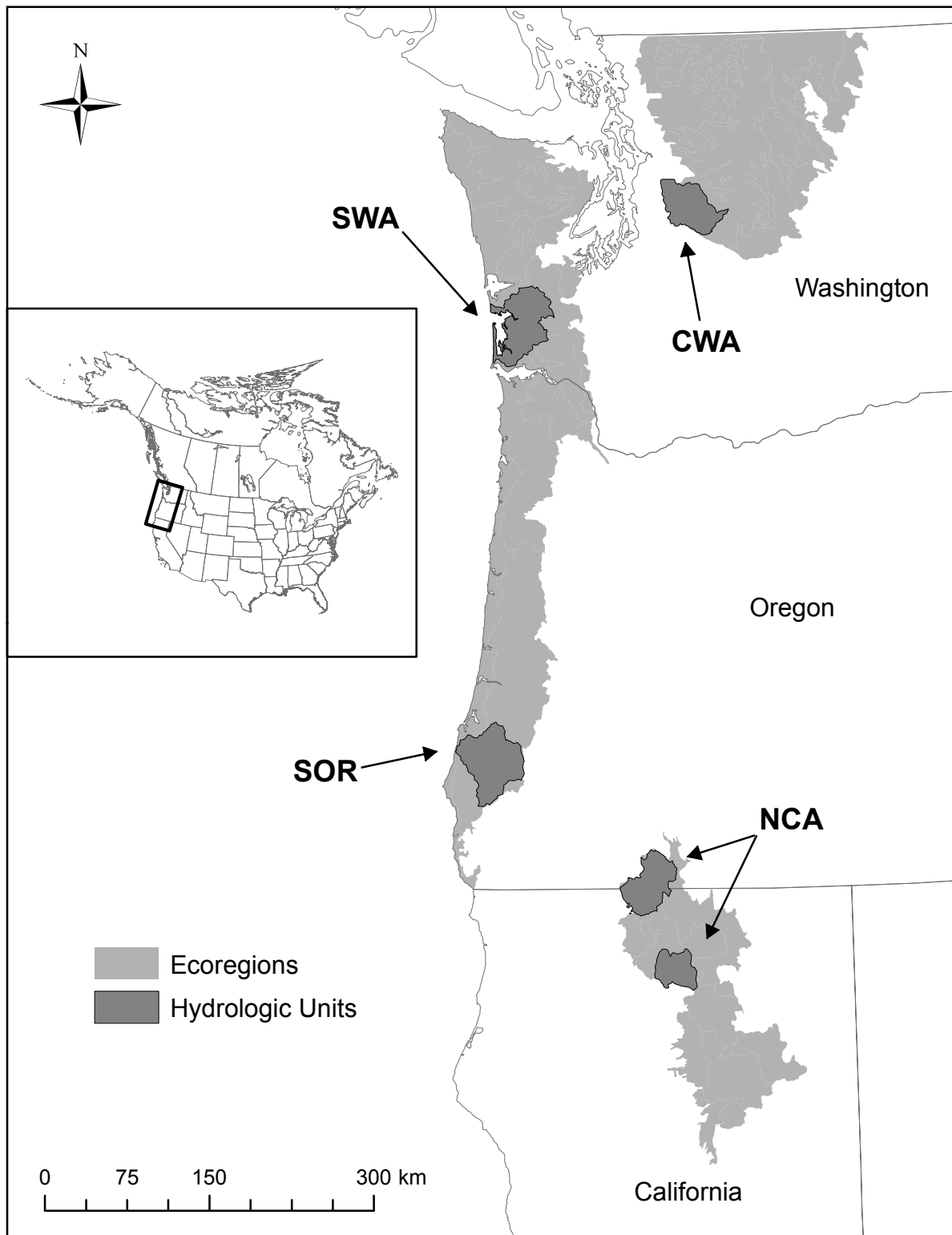


Figure 1.2. Mean probabilities of occupancy and detection for all species detected within the 4 regions during 2008 (filled squares) and 2009 (open squares). Each species-specific probability is defined by the mean of the posterior distribution for the intercept in the logit-linear models. Region codes represent the following areas in the Pacific Northwest: CWA = central Washington; SWA = southwest Washington; SOR = southwest Oregon; NCA = northern California.

Figure 1.2 (cont'd)

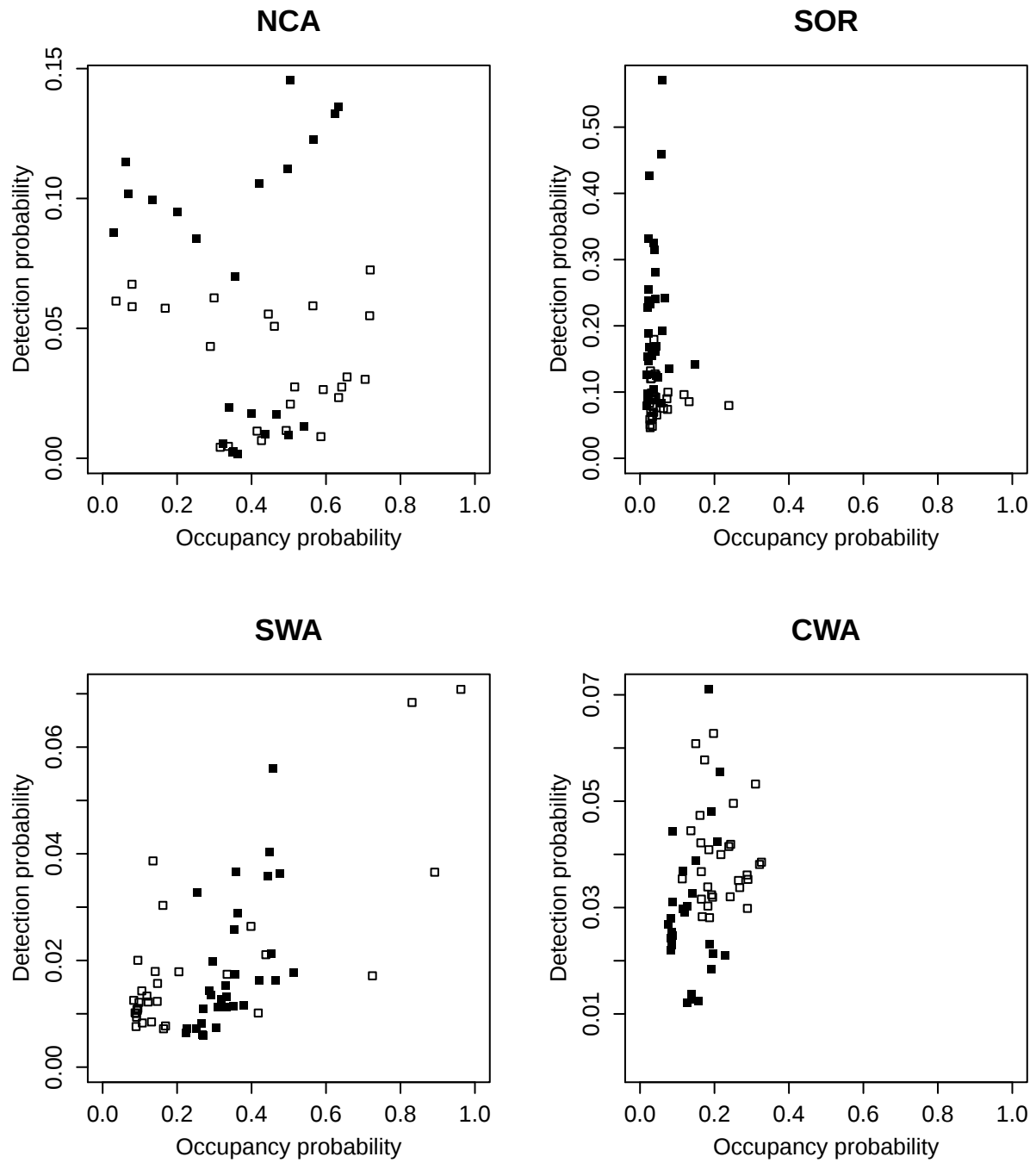


Figure 1.3. Posterior estimates (mean with 95% credible interval) of the regression coefficients from logit-linear models of detection for each species. The coefficients correspond to the following covariates: a) ordinal date, b) squared ordinal date, and c) previous detection. Species are ordered by increasing mean estimate of the coefficient and distinguished by habitat group into open/generalist species (open squares) and forest species (filled squares).

Figure 1.3 (cont'd)

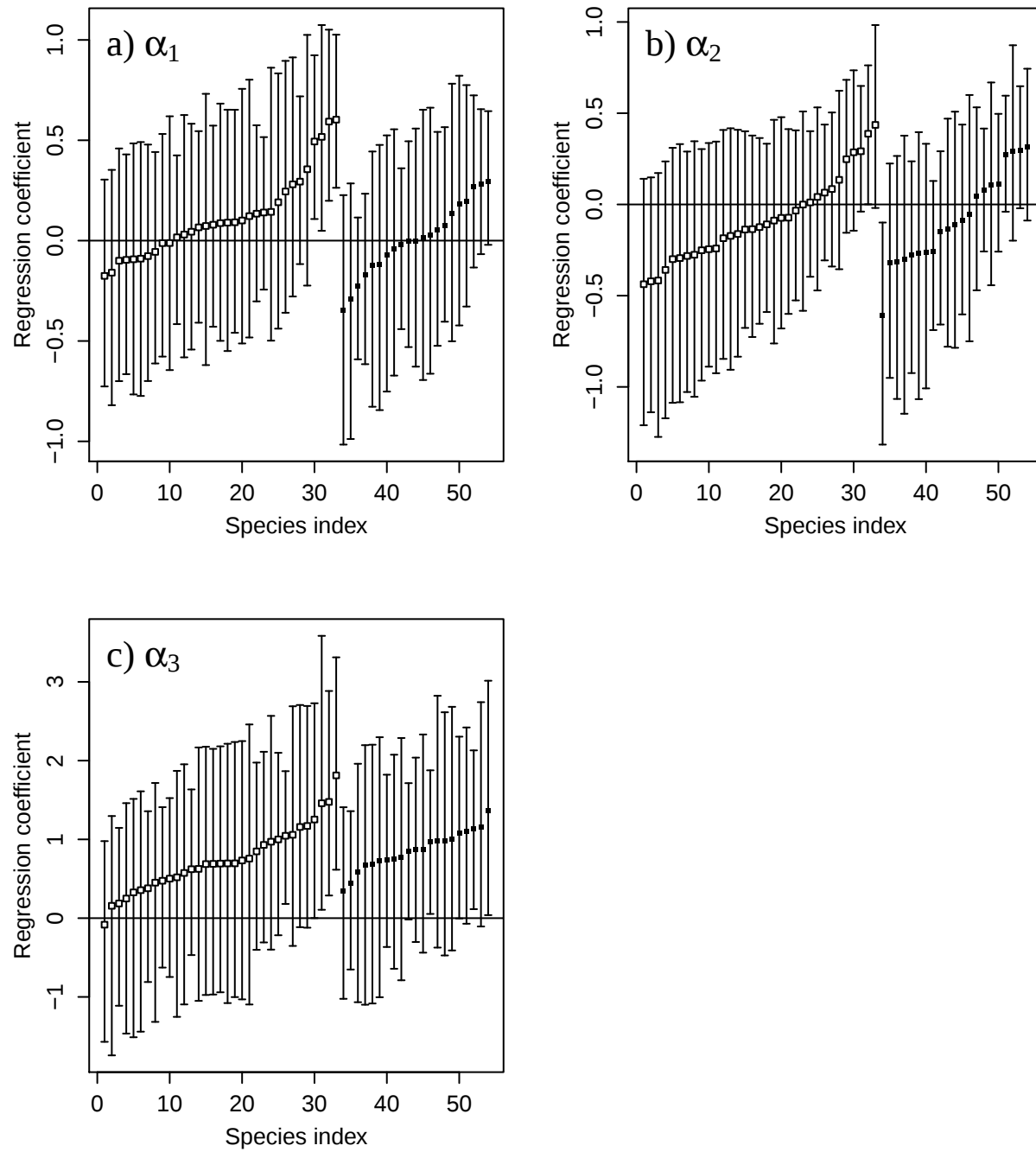


Figure 1.4. Posterior estimates (mean with 95% credible interval) of the regression coefficients from logit-linear models of occupancy for each species. The coefficients correspond to the following covariates: a) tree count, b) squared tree count, c) edge distance, and d) squared edge distance. Species are ordered by increasing mean estimate of the coefficient and distinguished by habitat group into open/generalist species (open squares) and forest species (filled squares).

Figure 1.4 (cont'd)

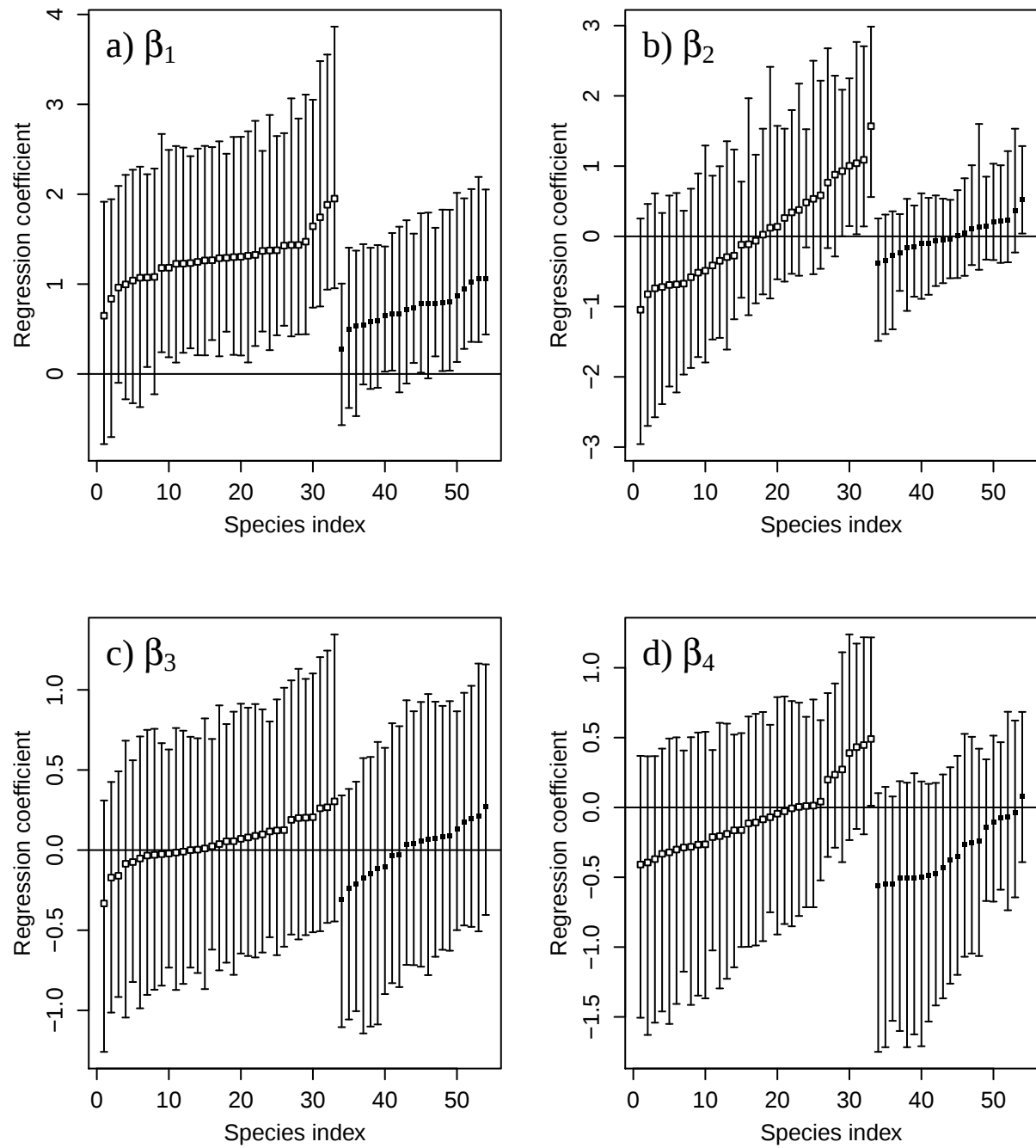


Figure 1.5. Mean estimated site richness for all species (a, b), forest species (c, d), and open/generalist species (e, f) at each retention site compared to tree count in 2008 (left) and 2009 (right). Study areas are colored with central Washington (CWA) = blue, southwest Washington (SWA) = green, southwest Oregon (SOR) = yellow, and northern California (NCA) = red. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

Figure 1.5 (cont'd)

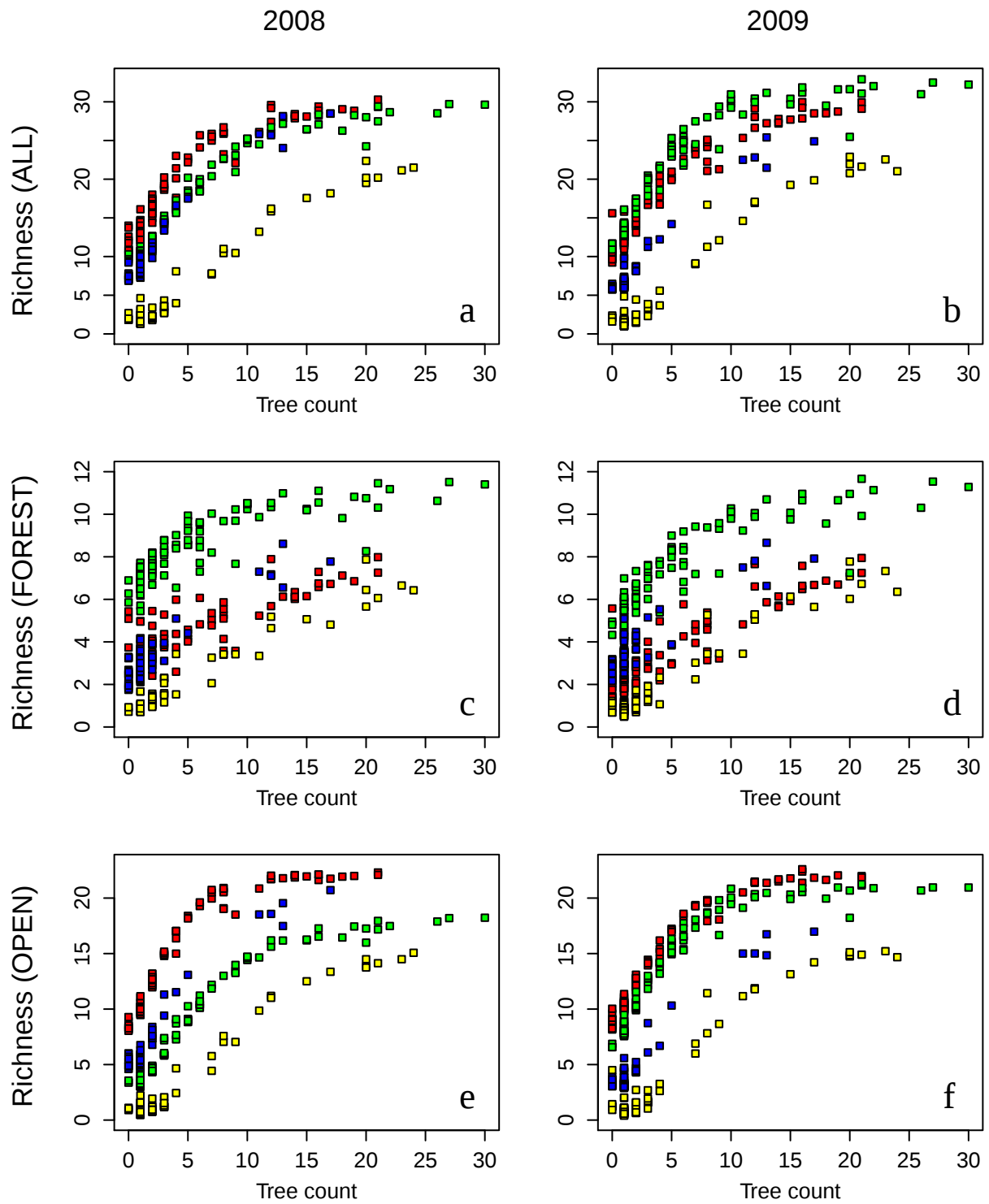
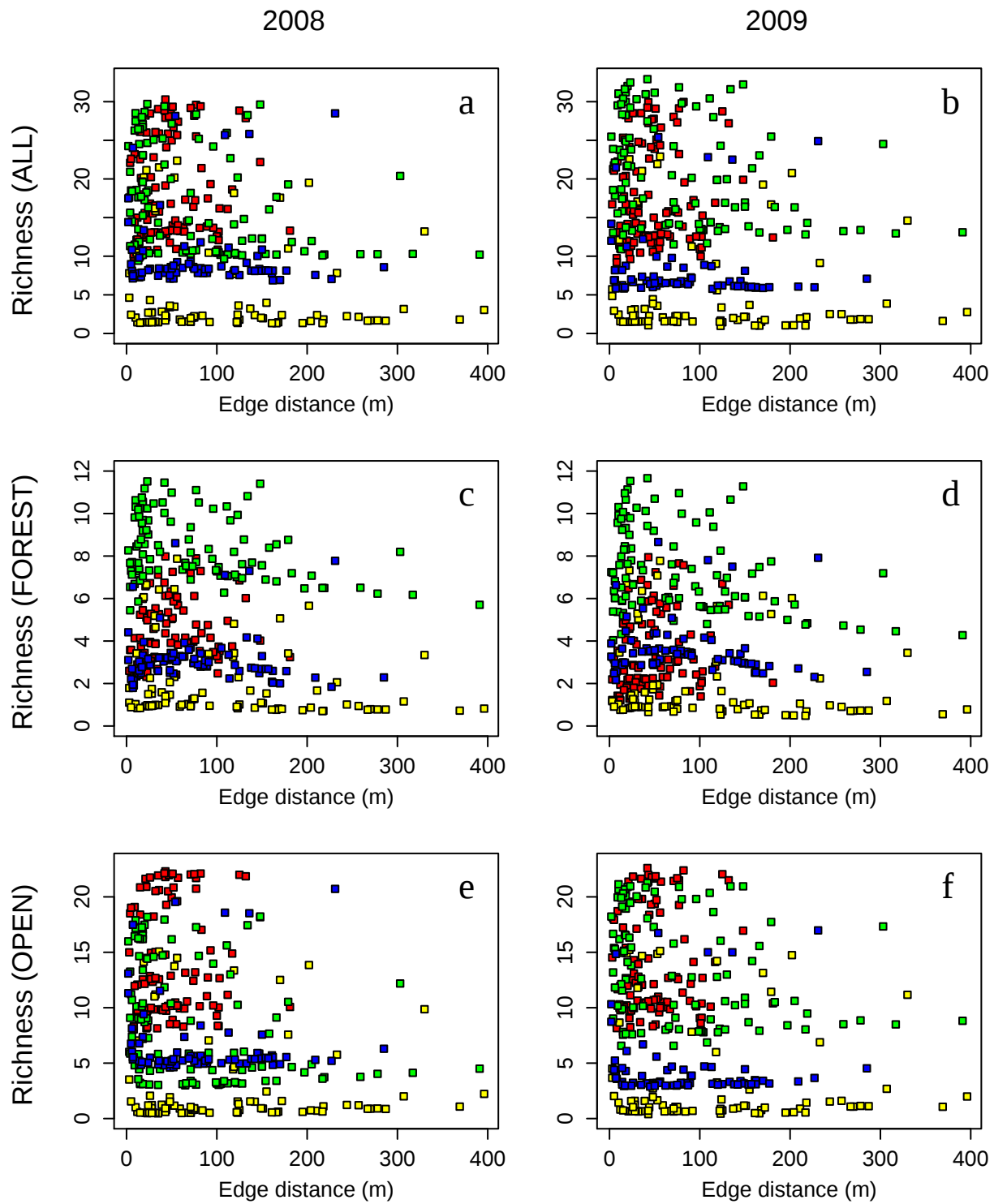


Figure 1.6. Mean estimated site richness for all species (a, b), forest species (c, d), and open/generalist species (e, f) at each retention site compared to edge distance (m) in 2008 (left) and 2009 (right). Study areas are colored with central Washington (CWA) = blue, southwest Washington (SWA) = green, southwest Oregon (SOR) = yellow, and northern California (NCA) = red.

Figure 1.6 (cont'd)



CHAPTER 2

MULTISTATE SITE OCCUPANCY ESTIMATION OF WHITE-HEADED WOODPECKERS

(*PICOIDES ALBOLARVATUS*) IN MANAGED FORESTS

Abstract

Structure retention is used to address biodiversity conservation objectives in managed forests by providing current and future snag resources for wildlife. The practice is considered critical to wildlife in intensively managed forests where timber production is the primary goal, but few studies have demonstrated a clear link between stand-level attributes of structure retention and metrics of species habitat use, such as occupancy and reproduction. In this study, we used a Bayesian multistate site occupancy model to understand how structure retention influences the probability of occupancy and nesting by white-headed woodpeckers (*Picoides albolarvatus*) on private industrial forests in California, USA during the 2010 breeding season. Our objective was to estimate state probabilities (i.e., occupancy and nesting) for white-headed woodpeckers at the harvest-unit scale and identify relationships between each state probability and habitat covariates that can be directly impacted by forest management decisions, including snag density in the harvest unit and proportion of mature forest on the landscape. Mean occupancy probability was estimated to be 0.98 (95% credible interval [CRI]: 0.89–1.00) and the probability of nesting given occupancy was 0.93 (95% CRI: 0.75–0.99), resulting in an unconditional nesting probability of 0.89 (95% CRI: 0.72–0.97). Snag density was positively associated with nesting probability, while neither covariate was good at predicting occupancy. The model indicated a negative effect of mature forest proportion on

nesting probability, though there was considerable uncertainty. Both detection of occupancy given nesting and detection of nesting increased with survey period, while detection of occupancy at sites without nesting decreased over time. The high occupancy and nesting probabilities in 2010 suggest that current structure retention policies have provided the necessary habitat conditions for white-headed woodpecker nesting in harvest units of northern California. Harvest units with >2 snags/ha (stem diameters >25.4 cm) had a probability of nesting that approached 1, suggesting a minimum threshold of retention that could serve as the biological basis for management targets.

Keywords: Bayesian framework, California, managed forests, multistate occupancy, nesting probability, structure retention, white-headed woodpecker

1. Introduction

Structure retention is a management practice that is recognized as critical to biodiversity conservation in managed forests (Bunnell *et al.*, 1999) given that legacy trees can create landscape-level structural diversity that might otherwise be lost (Franklin, 1989) and provide current and future snag resources for the numerous wildlife species that depend on them (Thomas *et al.*, 1979; Neitro *et al.*, 1985). Wildlife species that require dead and dying trees to meet certain life history requirements are negatively impacted by forest management actions that remove these resources, such as traditional even-aged timber harvesting (Bunnell *et al.*, 1999; Franklin *et al.*, 2002) and salvage logging after natural disturbances (Lindenmayer *et al.*, 2004; Lindenmayer and Noss, 2006). Cavity-nesting birds are especially vulnerable to silvicultural systems that do not provide the density and quality of snags necessary to maintain viable populations through time (Newton, 1994).

Primary cavity-nesters often have a disproportionately large influence on the diversity and abundance of bird species by acting as ecosystem engineers (Jones *et al.*, 1994), and some woodpeckers have been hypothesized to play the role of keystone species in forest ecosystems (Bednarz *et al.*, 2004; Martin *et al.*, 2004). Forest management practices that address the habitat needs of woodpeckers have the potential to affect entire species assemblages (Daily *et al.*, 1993; Drever and Martin, 2010). Examining the response by primary cavity-nesters to differences in stand-level snag resources may assist our understanding of the ecological benefit provided by structure retention in managed forests.

White-headed woodpeckers (*Picoides albolarvatus*) are a species that will likely benefit from forest practices that incorporate structure retention. This woodpecker is a

relatively weak primary excavator and an omnivore, requiring decayed snags for nesting and large, cone-producing pines (*Pinus* spp.) for foraging (Milne and Hejl, 1989; Dixon, 1995). The species is historically associated with old pine forests containing large diameter trees and an open canopy (Garrett *et al.*, 1996), though they have been found using managed forests with smaller diameter trees (Kozma, 2011). Pine seeds are considered a vital resource for overwinter survival of white-headed woodpeckers (Raphael and White, 1984), but they may also serve as the primary food item at other times of year, including the breeding season (Ligon, 1973; Dixon, 1995); forest types that support multiple species of cone-producing pines contain the highest abundance of white-headed woodpeckers (Garrett *et al.*, 1996). While the species is considered to be relatively common in California, it is “poorly studied” compared to other woodpeckers in North America (Garrett *et al.*, 1996) and considered a sensitive and/or threatened species by three states (Idaho, Oregon, Washington, USA) and the U.S. Forest Service. Several recent studies have increased our knowledge of white-headed woodpecker ecology (Wightman *et al.*, 2010; Hollenbeck *et al.*, 2011; Kozma, 2011) and suggest that forest disturbance events (e.g., wildfire) which increase snag density and decrease live tree cover can improve habitat quality for the species. In a previous study examining tree retention effects on bird communities, we observed frequent nesting by white-headed woodpeckers in clearcut harvest units with tree retention in northern California (D.W. Linden, personal observation). Identifying the factors that contribute to probability of nesting by white-headed woodpeckers in managed forests will help to guide retention policies for areas where the species occurs.

Occupancy modeling provides a method for estimating species occurrence probabilities and habitat relationships while accounting for imperfect detection, which has been recognized as an important and pervasive consideration for ecological studies attempting to understand species distributions (MacKenzie *et al.*, 2002; MacKenzie *et al.*, 2006). Failure to account for imperfect detection can bias both the estimates of species occurrence probabilities and the parameters of model covariates, such as habitat attributes (Gu and Swihart, 2004). While estimates of occupancy probability can improve understanding of species presence, presence alone may not be a particularly useful metric for evaluating conservation and management strategies that are aimed at impacting species persistence. A multistate occupancy model extends the basic scenario of presence/absence to situations where there is more than one category of species occupancy, such as the probability of reproduction given presence, and there is uncertainty about the true state of the species at a given site (Nichols *et al.*, 2007; MacKenzie *et al.*, 2009; Martin *et al.*, 2009). The model allows detection probabilities to vary according to the estimated true state, thus, accounting for differences in detection that might occur when certain states result in a species being more or less detectable (e.g., adult birds actively feeding young). More importantly, environmental covariates that influence the state probabilities can be evaluated in the model.

We used a multistate occupancy model to estimate probabilities of occurrence and reproduction of white-headed woodpeckers within an intensively managed forest landscape in northern California, USA. The multistate model allowed us to examine how forest management practices that impact stand- and landscape-level habitat attributes might influence state probabilities, while accounting for differences in detection

probability that might result from changes in nesting behavior during the breeding season (Russell *et al.*, 2009b). Our objective was to estimate occupancy and nesting probabilities of white-headed woodpeckers at the harvest-unit scale and identify relationships between each state probability and habitat covariates that can be directly impacted by forest management decisions, including snag density in the harvest unit and proportion of mature forest on the landscape. We hypothesized that white-headed woodpeckers would have higher occupancy and nesting probabilities in harvest units that retained greater densities of snags having a diameter at breast height (dbh) >25.4cm due to increased availability of nest sites (Milne and Hejl, 1989; Kozma, 2009; Wightman *et al.*, 2010). In addition, we hypothesized that both state probabilities would be positively associated with the proportion of mature forest with large diameter trees (e.g., >50cm) surrounding the harvest units (1-km radius) that could be used as foraging habitat for white-headed woodpeckers during fall and winter, but may also serve as an important resource during the breeding season (Dixon, 1995).

2. Methods

2.1. Study area

We conducted the study in northern California, east of Mt. Shasta, on private industrial timberlands surrounded by the Shasta-Trinity National Forest (centered around 41°21'N, 121°50'W)(Figure 2.1). The area was covered by second- and third-growth, mixed-conifer forest that was historically dominated by ponderosa pine (*Pinus ponderosa*) and is now mostly white fir (*Abies concolor*). Selective logging and fire suppression in the last century have altered the overstory composition similar to other dry forests of western

North America (Hessburg *et al.*, 2005). Additional overstory species (in decreasing order of prevalence) included Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), California incense-cedar (*Calocedrus decurrens*) and sugar pine (*Pinus lambertiana*), and non-forested areas were typically chaparral vegetation composed primarily of manzanita (*Arctostaphylos spp.*). True fir (*Abies spp.*) dominance generally increased with elevation, and elevations ranged from 1250–1950m. The study area was characterized by a mosaic of stand size classes: ~41% was comprised of mature stands with a quadratic mean diameter (QMD; diameter of tree with average basal area) >60cm, ~36% contained younger stands with a QMD ranging 25–60cm, and the remaining ~20% of stands were evenly split among past harvests (QMD = 12–25cm), relatively recent harvests (QMD = 3–12cm) and new harvests (planted with seedlings)(U.S. Forest Service, 2007).

We selected all harvest units that were clearcut with retention between 3–6 yrs prior to 2010 in the study area (n=65). Recent harvests (<1 yr old) were not selected to avoid potential disturbance effects from harvesting and replanting activities. Harvest units had a mean area = 9ha (range = 4–15ha) and typically contained 1–6 patches (~0.1ha) of green-tree retention that were randomly dispersed throughout the unit, in addition to varying densities of snags that were retained during harvest (including stumps >1m tall).

2.2. Woodpecker surveys

We used repeated, independent surveys across multiple visits to each harvest unit from June–July 2010 to estimate state and detection probabilities for white-headed woodpeckers. During each survey, a single observer walked to the center of the harvest unit and after a 2-min settling period, recorded all detections of woodpeckers in the harvest unit over a 10-min observation period. Sex and behavior of detected individuals

were recorded when possible and detections that occurred before or after the 10-min period (typically while entering/exiting the harvest unit) were recorded separately. We used passive as opposed to broadcast surveys (Dudley and Saab, 2003) to prevent individuals in nearby harvest units from being enticed into entering the focal harvest unit. At the conclusion of the 10-min observation, areas of the harvest unit where woodpecker behavior suggested the presence of a nest (e.g., individuals viewed carrying food or entering a snag cavity) were searched and carefully observed for up to 30min or until a nest was located. All surveys were conducted between sunrise and 5 hours post under optimal weather conditions (e.g., no rain or heavy wind). Intervals between surveys were approximately 7–10 days with a maximum of 4 visits to each harvest unit.

We used a removal design (Farnsworth *et al.*, 2002) to construct a detection history (see *Modeling framework*) for each harvest unit, where visits to a given site were terminated once evidence of reproduction was found. This design recognizes that subsequent detection of a state may lack independence from previous detections under certain circumstances, as in this case, due to observer experience of finding a nest. This heterogeneity in detection probability could be modeled explicitly but would not increase the precision of estimates for the state and detection probabilities, nor provide any additional useful information (MacKenzie and Royle, 2005; Saracco *et al.*, 2011).

2.2. Habitat covariates

We used a combination of field-collected and remotely-sensed data to describe the habitat covariates we hypothesized would influence the state probabilities of occupancy and nesting. Snag density was measured at each harvest unit by a complete tally of all dead wood >12.7cm dbh and >1m tall. Previous experience with white-headed woodpeckers at

these sites suggested tall stumps were a frequently used substrate for cavity nests and, thus, were tallied with standing snags. Snags <5m outside the harvest unit boundary were also included. We used a Geographic Information System (GIS) to determine boundaries of harvest units by examining shapefiles outlining Timber Harvest Plans (THPs) as provided by the California Department of Forestry (<ftp://ftp.fire.ca.gov/forest/>) and 2009 aerial photography from the National Agricultural Imagery Program (NAIP; <http://datagateway.nrcs.usda.gov/>). Snag tallies for stems >25.4cm diameter were divided by the estimated area of the harvest unit to derive the snag density; the diameter cutoff represented the lower limit for white-headed woodpecker cavity nests observed in the field and in previous studies (Milne and Hejl, 1989; Kozma, 2009).

We calculated the proportion of mature forest within a 1-km radius from the center of each harvest unit within a GIS to estimate the availability of large trees for foraging. Mature forest was designated by areas containing trees with a mean dbh >60cm, as determined by the California Wildlife Habitat Relationships (CWHHR) classification provided in the CALVEG geodatabase (U.S. Forest Service, 2007). The 1-km radius represented the estimated home range of a white-headed woodpecker (Garrett *et al.*, 1996; Hollenbeck *et al.*, 2011). We considered using forest patches that were pine dominant according to the CALVEG geodatabase, but these forest types were relatively rare at the higher elevations typical of our study area where true firs were the most numerous tree species. We acknowledge that our classification of mature forest did not guarantee the presence of large diameter pines, though they were frequently observed in the forests surrounding our harvest units (including a >250cm dbh sugar pine; D. W. Linden, personal observation).

2.4. Modeling framework

We developed a multistate model using the hierarchical modeling framework presented by Royle and Dorazio (2008) and following the notation of Nichols *et al.* (2007) for estimating occupancy with multiple states. Here we considered each harvest unit to represent one of $i = 1, \dots, N = 65$ sites each with $j = 1, \dots, J = 4$ surveys. Each of the 4 survey intervals spanned 10 days, during which a site could be visited no more than once depending on whether a previous visit had detected a nest. The observed state at site i could be categorized into 1 of 3 states (m): unoccupied ($m = 0$); occupied without nesting ($m = 1$); and occupied with nesting ($m = 2$).

We modeled detections conditional on the latent true state such that $y_{ij}|z_i \sim \text{Bern}(z_i p_j^m)$, where y_{ij} is the observed state (m) at site i during survey j , z_i is the latent true state at site i , and p_j^m is the probability of detecting state m during survey j . We used the notation of Nichols *et al.* (2007) which reparameterizes the detection probabilities such that: p_j^1 = the probability of detecting occupancy given that the site is occupied without nesting = $\Pr(y_{ij} = 1|z_i = 1)$; p_j^2 = the probability of detecting occupancy given that the site is occupied with nesting = $\Pr(y_{ij} = 1|z_i = 2)$; and δ_j = the probability of detecting a nest given that the site is occupied with nesting = $\Pr(y_{ij} = 2|z_i = 2)$. Detection histories for each site, $\mathbf{y}_i$, consisted of $J = 4$ surveys regardless of whether the site was actually visited 4 times; if a site was not visited during survey interval j then $y_{ij} = \text{NA}$.

We modeled the latent true occupancy state such that $z_i \sim \text{Bern}(\psi_i^m)$, where ψ_i^m is the probability of occupancy state m at site i . Once again, we followed the Nichols *et al.*

(2007) notation that reparameterizes a more general multinomial occupancy model (MacKenzie *et al.*, 2009) where the state probabilities are defined as follows: ψ_i^1 = the probability that site i is occupied ($m = 1$ or 2) = $\Pr(z_i = 1) + \Pr(z_i = 2)$; and ψ_i^2 = the probability that site i has a nest ($m = 2$), given that the site is occupied ($m = 1$ or 2) = $\Pr(z_i = 2) / (\Pr(z_i = 1) + \Pr(z_i = 2))$. The unconditional nesting probability is specified as $\psi_i^{1*2} = \psi_i^1 \times \psi_i^2$. This parameterization allows for the examination of covariates affecting each probability separately (Nichols *et al.*, 2007), which is more biologically interesting than examining relationships with the unconditional probability of occupancy without nesting, $\Pr(z_i = 1)$ (MacKenzie *et al.*, 2009).

We examined the effects of covariates on state and detection probabilities using logit-linear models. Detection probabilities were modeled as follows:

$$\text{logit}(p_j^1) = \alpha_{10} + \alpha_{11} \text{survey}_j$$

$$\text{logit}(p_j^2) = \alpha_{20} + \alpha_{21} \text{survey}_j$$

$$\text{logit}(\delta_j) = \alpha_{30} + \alpha_{31} \text{survey}_j$$

where α_{10} , α_{20} , and α_{30} are the logit-transformed detection probabilities; and α_{11} , α_{21} , and α_{31} are the regression coefficients for the variable survey_j which simply indexes the survey number ($j = 1, 2, 3$, or 4) and allows for the detection probabilities to increase, decrease, or remain constant over the course of the entire study. We hypothesized that the detection probabilities p_j^2 and δ_j would increase over the survey intervals as woodpeckers became more conspicuous during nesting activities that required frequent movement (e.g., returning to cavity nest to feed young).

Our logit-linear models for the occupancy state probabilities were as follows:

$$\text{logit}(\psi_i^1) = \beta_{10} + \beta_{11}snags_i + \beta_{12}forest_i$$

$$\text{logit}(\psi_i^2) = \beta_{20} + \beta_{21}snags_i + \beta_{22}forest_i$$

where β_{10} and β_{20} are the logit-transformed probabilities of occupancy and nesting given occupancy, respectively; β_{11} and β_{21} are regression coefficients for the variable $snags_i$, representing the snag density at site i ; and β_{12} and β_{22} are regression coefficients for the variable $forest_i$, which describes the proportion of mature forest in a 1-km radius around site i . We considered quadratic terms for $forest_i$ but this relationship was not supported by the data for either state probability and thus, we removed it for simplicity. All covariates were standardized to have a mean of 0 and unit variance of 1 to facilitate comparison of effect sizes between the selected covariates.

We incorporated spatial random effects into our logit-linear models for the occupancy state probabilities, given that our distribution of sites and average distance between sites was small relative to the dispersal capability and home-range size of white-headed woodpeckers, such that we might expect some spatial autocorrelation in the state probabilities. The spatial random effects could potentially account for unmeasured environmental covariates or spatial population processes (e.g., source-sink dynamics) that affected the species distribution in our study area (Chelgren *et al.*, 2011). Therefore, the logit-linear models for ψ_i^1 and ψ_i^2 included additional terms, β_{13i} and β_{23i} , representing zero-mean random variables that were spatial correlated with distance according to an exponential function (Diggle *et al.*, 1998, as referenced in Chelgren *et al.*, 2011). These spatial random effects were each assigned multivariate normal distributions, such that

$\beta_{13i} \sim \text{MVN}(0, \sigma_1^2 \Sigma)$ and $\beta_{23i} \sim \text{MVN}(0, \sigma_2^2 \Sigma)$; the variance terms σ_1^2 and σ_2^2 serve as the variances of the random effects, while Σ is the between-site correlation matrix. The elements of the $N \times N$ correlation matrix were calculated by an exponential function, $\exp(-\phi d_{i1, i2})$ where ϕ controls the rate of decay in correlation between any 2 sites separated by distance $d_{i1, i2}$; larger values of ϕ result in a more rapid decay. It should be noted that we chose the same correlation matrix for each of the spatial random effects, but allowed the variances to differ.

We implemented the multistate model in WinBUGS (Spiegelhalter *et al.*, 2003), using the R2WinBUGS package (Sturtz *et al.*, 2005) from R (R Development Core Team 2011). WinBUGS is a software program designed for Bayesian model inference using Markov chain Monte Carlo (MCMC) methods with Gibbs sampling (Geman and Geman, 1984) to estimate model parameters by sampling from the joint probability distribution. Posterior distributions for all model parameters are estimated, from which means and credible intervals (CRIs – the Bayesian equivalent to a confidence interval) can be calculated. The model specification easily facilitates the incorporation of spatial random effects. We used non-informative priors for most model parameters in the logit-linear models, including a uniform distribution between 0 and 1 on the probability scale for intercepts ($\alpha_{10}, \alpha_{20}, \alpha_{30}, \beta_{10}, \beta_{20}$) and a normal distribution with mean = 0 and variance = 100 for covariates of detection ($\alpha_{11}, \alpha_{21}, \alpha_{31}$) and occupancy state ($\beta_{11}, \beta_{21}, \beta_{12}, \beta_{22}$). Similar to Chelgren *et al.* (2011), we found the terms for the spatial random effects to be particularly sensitive and were unable to use typical uninformative priors on those parameters. The priors we used for σ_1^2 and σ_2^2 were hierarchical half-

normal (mean = 0, variance = v^2 , df = 1) with a uniform U(0, 1) prior on v ; this specification recognizes that the spatial random effects are likely small with low variance (Gelman, 2006). Our prior for ϕ was uniform U(1,30) which dictated a reasonable range in magnitude of correlation with increasing distance between sites; for example, the range in potential correlation for sites separated by 0.5km was 0.28–0.96, while for sites separated by 10km it was 0–0.42 (for context, see Figure 2.1).

We examined posterior distributions for model parameters by running 3 chains of 100,000 iterations, discarding the first 50,000 iterations, and thinning by 25; this resulted in 6,000 values forming the posterior distribution for each model parameter. We assessed model convergence by examining trace plots and ensured that the scale reduction factor, or R-hat statistic, was <1.1 and the effective sample size was >100 for all model parameters (Gelman and Hill, 2007). We assessed the significance of regression coefficients based on whether the estimated credible intervals overlapped zero; strong support for a covariate effect was indicated when the 95% CRI did not overlap zero, while weak support was indicated when the 90% CRI did not overlap zero. WinBUGS code for model specification is presented in the Appendix (A.2).

3. Results

We detected white-headed woodpeckers at 58 of the 65 harvest units and found cavity nests at 42 harvest units, resulting in a naïve estimate of 0.89 (95% CRI: 0.79–0.95) for occupancy probability and 0.72 (95% CRI: 0.60–0.82) for nesting probability, given occupancy. We detected nests across all 4 survey intervals, but only 5 harvest units were discovered to have nesting in the last survey. Snag densities (for trees >25.4cm dbh)

averaged 3.35 snags/ha (standard deviation [SD]: 2.55, range: 0.24–12.53) within harvest units while the proportion of mature forest surrounding harvest units (1km-radius) averaged 0.45 (SD: 0.19, range: 0–0.87). A simple logistic regression comparing harvest units with detected nests to those without revealed no significant effects of snag density or proportion of mature forest on naïve nesting probability.

The hierarchical multistate model which accounted for imperfect detection suggested higher estimates for both occupancy and nesting probabilities, with $\psi_i^1 = 0.98$ (95% CRI: 0.89–1.00) and $\psi_i^2 = 0.93$ (95% CRI: 0.75–0.99) for sites with average values of the covariates. For the unconditional probability of nesting in the study area, $\psi_i^1 * 2 = 0.89$ (95% CRI: 0.72–0.97). Model results suggested only one covariate with strong support (95% CRI not overlapping zero) for a relationship with state probability – snag density, which appeared to increase the conditional nesting probability (Table 2.1). Examination of the change in predicted nesting probability with increasing snag density indicates that the probability of a white-headed woodpecker nesting in a harvest unit approaches 1 at densities >2 snags/ha (Figure 2.2). The model also suggested weak support (90% CRI not overlapping zero) for a relationship between conditional nesting probability and proportion of mature forest; conditional probability of nesting appeared to decrease with an increasing proportion of mature forest, though uncertainty in the predicted probability is evident at high proportions (Figure 2.3).

Detection probabilities were variable depending on the estimated true state and the survey interval (Table 2.1; Figure 2.4). While none of the linear trends with survey interval had strong support, all had weak support from the data. The probability of detecting

occupancy by white-headed woodpeckers was considerably lower for sites that did not contain a nest than for sites that did (Figure 2.4). In addition, the detection probability decreased over time for sites without nesting and increased for sites with nesting; p_j^1 ranged from 0.46 (95% CRI: 0.23–0.71) in survey 1 to 0.17 (95% CRI: 0.01–0.50) in survey 4, while p_j^2 ranged from 0.79 (95% CRI: 0.68–0.88) in survey 1 to 0.95 (95% CRI: 0.82–0.99) in survey 4 (Figure 2.4). The probability of detecting a nest also increased with time and ranged from 0.42 (95% CRI: 0.30–0.55) in survey 1 to 0.66 (95% CRI: 0.48–0.85) in survey 4.

4. Discussion

Structure retention in harvest units is considered to be a critical component of biodiversity conservation in managed forests (Bunnell and Huggard, 1999), yet little information exists regarding the response by wildlife species to specific practices within intensively managed landscapes where timber production is the primary goal. Our results suggest that white-headed woodpeckers had a high probability of occupancy across young (3–6 yr old) harvest units that employed structure retention and that the density of retained snags was a significant predictor of woodpecker nesting probability in industrial forests of northern California. Our study illustrates the tangible benefits of structure retention to the population persistence of a primary cavity-nester and suggests biologically-based targets for retention policies that can impact avian communities.

We found evidence for our hypothesis that nest-site availability might be limiting in harvest units and those units with higher densities of retained snags would be more likely to contain a white-headed woodpecker nest. Other studies of white-headed woodpeckers

have suggested that decay condition may be more important than density of snags (Raphael and White, 1984; Wightman *et al.*, 2010), given that not all snags are considered available for nest sites when the condition of the wood is unsuitable for cavity excavation (Bagne *et al.*, 2008). Snag decay condition increases with the time-since-death of the tree but also interacts with cause of death (e.g., fire vs. insect) and tree species (Morrison and Raphael, 1993). We did not include snag decay condition or species in our model due to the lack of variation across harvest units in our study: for snags >25.4cm dbh, 97% were in moderate to late stages of decay and 86% were true fir (*Abies* spp.). Thus, we felt snag density was an appropriate proxy for nest-site availability and chose the 25.4cm dbh threshold to reflect white-headed woodpecker nest-site preferences demonstrated by previous studies (Milne and Hejl, 1989) and our own observations (95% of nest trees >25.4cm dbh [n=89], D. W. Linden, unpublished data).

The model indicated weak support for a negative relationship between mature forest proportion within a 1-km radius and white-headed woodpecker nesting probability. This result was counter to our hypothesis that mature forest, defined by stands with an average diameter >60cm, may provide foraging habitat for white-headed woodpeckers and increase the probability that a harvest unit would be occupied and contain a nest. Previous studies have cited the importance of large-diameter pine forests as foraging habitat for white-headed woodpeckers due to their reliance on pine seeds during the winter and throughout the year (Dixon, 1995; Garrett *et al.*, 1996; Kozma, 2011). The study area supported multiple pine species (e.g., ponderosa and sugar), yet the forest composition was dominated by firs and the remotely-sensed data could not predict the location of individual mature pine trees; thus, our definition of mature forest may have been over-

simplified. Hollenbeck *et al.* (2011) found that QMD was a predictor of white-headed woodpecker habitat in Oregon but acknowledged both the limitation of remotely-sensed data for estimating QMD and the possibility that QMD did not properly quantify the presence of large-diameter pines. At the stand level, canopy cover within mature forests in our study area was consistently high (>60%) and would not qualify as the “open canopy” that white-headed woodpeckers appear to prefer (Garrett *et al.*, 1996). At the landscape scale, a uniform pattern of harvest units resulting from state forest practices rules, which restrict the adjacency of timber harvests (California Department of Forestry and Fire Protection, 2007), may have created a suitable juxtaposition of open and closed forests (Hollenbeck *et al.*, 2011) and provided the necessary conditions for white-headed woodpecker nesting. This would explain why the proportion of mature forest decreased nesting probability, as higher proportions effectively eliminate that juxtaposition.

We used a hierarchical multistate occupancy model (Nichols *et al.*, 2007; MacKenzie *et al.*, 2009) to estimate the probability of multiple species states, specifically occupancy and nesting, while accounting for imperfect detection and state uncertainty. The multistate model estimated detection probability both for the presence of individuals and the presence of cavity nests, allowing us to distinguish differences between detection processes that were dependent on the true state of the species at the site. The detection probabilities of occupancy and nesting for sites with a nest suggested that woodpeckers were more likely to be detected as the breeding season progressed, which may have been a function of changes in behavior due to the activities associated with rearing young. Given that detection probabilities were <1, a failure to incorporate detection would have led to biased estimates of the state probabilities. A simple logistic regression suggested that the

naïve estimate of overall nesting probability of white-headed woodpeckers in young harvest units was 0.65, much lower than the probability estimate from the multistate model ($\psi_i^1 * 2 = 0.89$). The differences in occupancy probability between the simple model (0.89) and multistate model ($\psi_i^1 = 0.98$) were smaller, suggesting that state uncertainty was responsible for more bias than imperfect detection. The simple model also found that snag density was not a good predictor of nesting which opposed the significant relationship estimated by the multistate model and further illustrates the bias that can occur with regression coefficients when imperfect detection is ignored in presence/absence models (Gu and Swihart, 2004).

Our estimates of white-headed woodpecker occupancy and nesting probability are restricted to young harvest units (3–6 yrs old) during the breeding season in 2010, which limits some of our inference. We did not survey recent harvest units (<1 yr old) due to concerns over the impact of the recent disturbance on nest site selection, though we acknowledge that woodpeckers may have been using the new cuts. Anecdotally, we observed a successful white-headed woodpecker nest in one unit that had been harvested between the 2009 and 2010 breeding seasons which indicates non-zero occupancy and nesting probabilities in new harvest units. We also did not survey older harvest units (10–15 yrs old) which prevented us from examining how occupancy changes over time, though we expect detection probability would have been severely decreased in older cuts given that regeneration in these units was often >2–3m in height and our survey methods relied on a clear view of the entire harvest unit. Based on previous observations in the study area, we suspect that decreased snag densities, due to longer decay periods, and increased

cover for nest predators likely decreased the probability of white-headed woodpecker nesting in older harvest units.

5. Management implications

Our study supports the ecological benefit of structure retention in managed forests, as illustrated by white-headed woodpecker nesting in harvest units of northern California. Results from the multistate occupancy model suggest that nesting probability was significantly increased by the retained snag density in harvest units, with probabilities approaching 1 at >2 snags/ha (stems >25.4 cm dbh). State forest practices rules in California require the retention of all non-merchantable safe snags during harvest (California Department of Forestry and Fire Protection, 2007). This policy appears to be providing the habitat conditions necessary for supporting white-headed woodpeckers in dry conifer forests of northern California, given the high estimates of occupancy (0.98) and overall nesting probability (0.89). Where safety concerns or site conditions prevent the retention of natural snags, high-cut stumps (≥ 2 m in height) may provide an easy and effective alternative given the propensity by white-headed woodpeckers to create cavity nests relatively close to the ground (<3 m; Milne and Hejl, 1989), though these created snags may take 3–5 years or longer before they are suitable for cavity excavation (Arnett *et al.*, 2010). Additional research should identify links between white-headed woodpeckers and secondary cavity-nesters to understand whether management practices that support these woodpeckers can also support other members of the avian community.

Table 2.1. Posterior summaries for model parameters (means, standard deviations [SD], and 95% credible intervals [lower = 0.025, upper = 0.975]) from the multistate model estimating white-headed woodpecker occupancy and nesting probabilities during 2010 among harvest units in California, USA. Parameters include intercepts and regression coefficients (of standardized variables) from the logit-linear models for probabilities of occupancy (ψ_i^1), nesting given occupancy (ψ_i^2), detection of occupancy given the site is occupied without nesting (p_j^1), detection of occupancy given the site is occupied with nesting (p_j^2), and detection of nesting given the site is occupied with nesting (δ_j).

Table 2.1 (cont'd)

Parameter	Mean	SD	0.025	0.975
Occupancy (ψ_i^1)				
β_{10}	3.942	1.261	2.110	6.944
β_{11} (<i>snags_i</i> effect)	0.678	1.065	-1.680	2.605
β_{12} (<i>forest_i</i> effect)	1.003	0.904	-0.890	2.719
Nesting occupancy (ψ_i^2)				
β_{20}	2.641	0.940	1.116	4.790
β_{21} (<i>snags_i</i> effect)	3.088	1.151	1.116	5.714
β_{22} (<i>forest_i</i> effect)	-1.366	0.797	-3.063	0.099
Detection of occupancy occupancy without nesting (p_j^1)				
α_{10}	0.394	0.904	-1.306	2.295
α_{11} (<i>survey_j</i> effect)	0.751	0.653	-0.581	2.024
Detection of occupancy occupancy with nesting (p_j^2)				
α_{20}	-0.558	0.543	-1.964	0.179
α_{21} (<i>survey_j</i> effect)	0.584	0.403	-0.103	1.474
Detection of nesting occupancy with nesting (δ_j)				
α_{30}	-0.675	0.518	-1.741	0.304
α_{31} (<i>survey_j</i> effect)	0.354	0.255	-0.072	0.885

Figure 2.1. Harvest units selected to survey white-headed woodpecker occurrence and reproduction during 2010 near Mt. Shasta, California, USA.

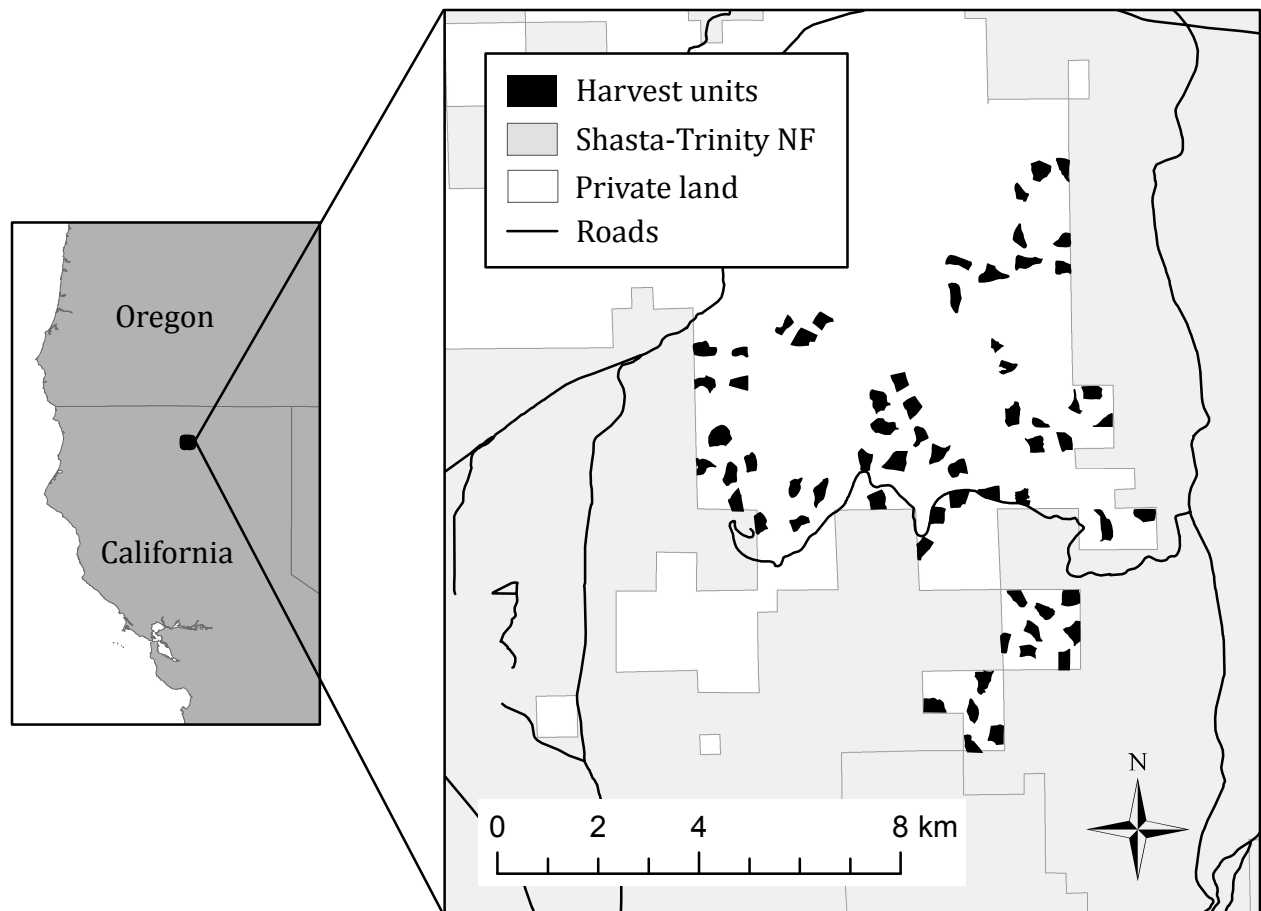


Figure 2.2. Model predicted relationship between conditional nesting probability, ψ_i^2 , of white-headed woodpeckers and harvest unit snag density (snags >25.4cm diameter/ha) on industrial timberlands in northern California. Mean probability with 95% credible intervals are presented.

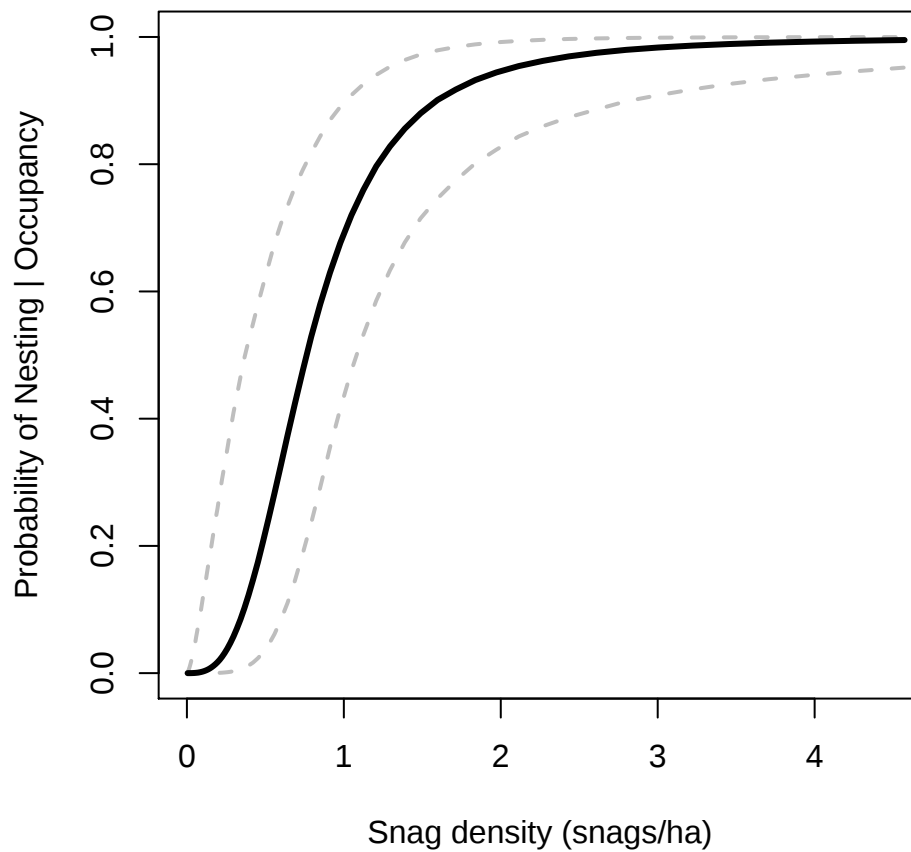


Figure 2.3. Model predicted relationship between conditional nesting probability, ψ_i^2 , of white-headed woodpeckers and proportion of mature forest (quadratic mean diameter >60cm) within a 1-km radius on industrial timberlands in northern California. Mean probability with 95% credible intervals are presented.

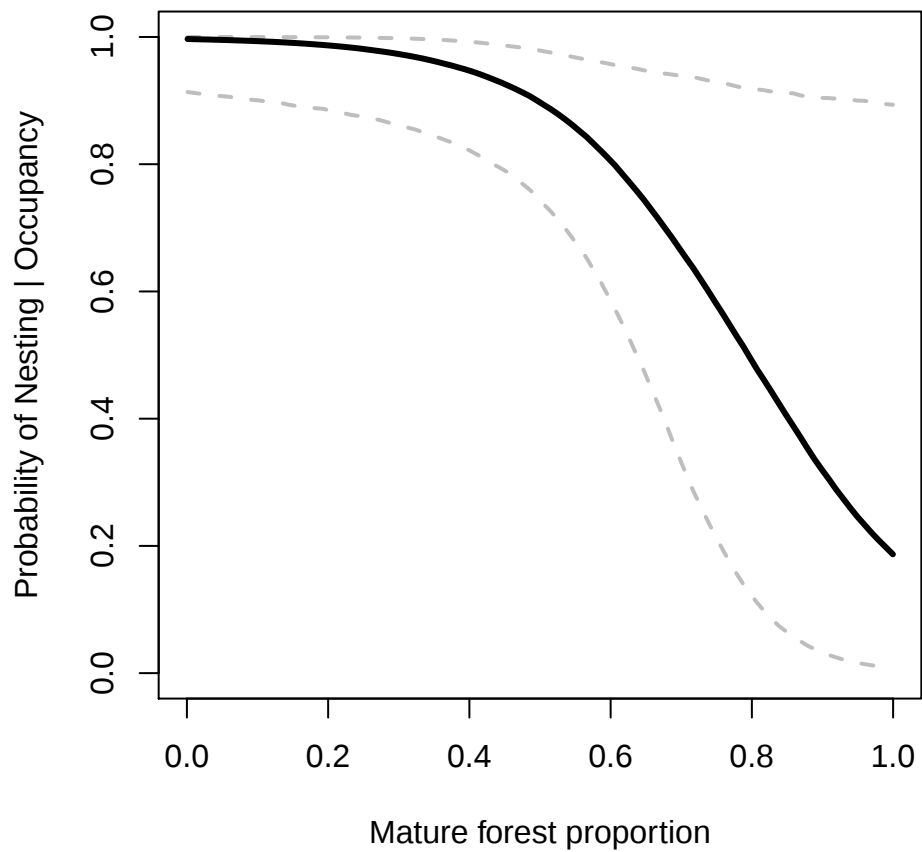
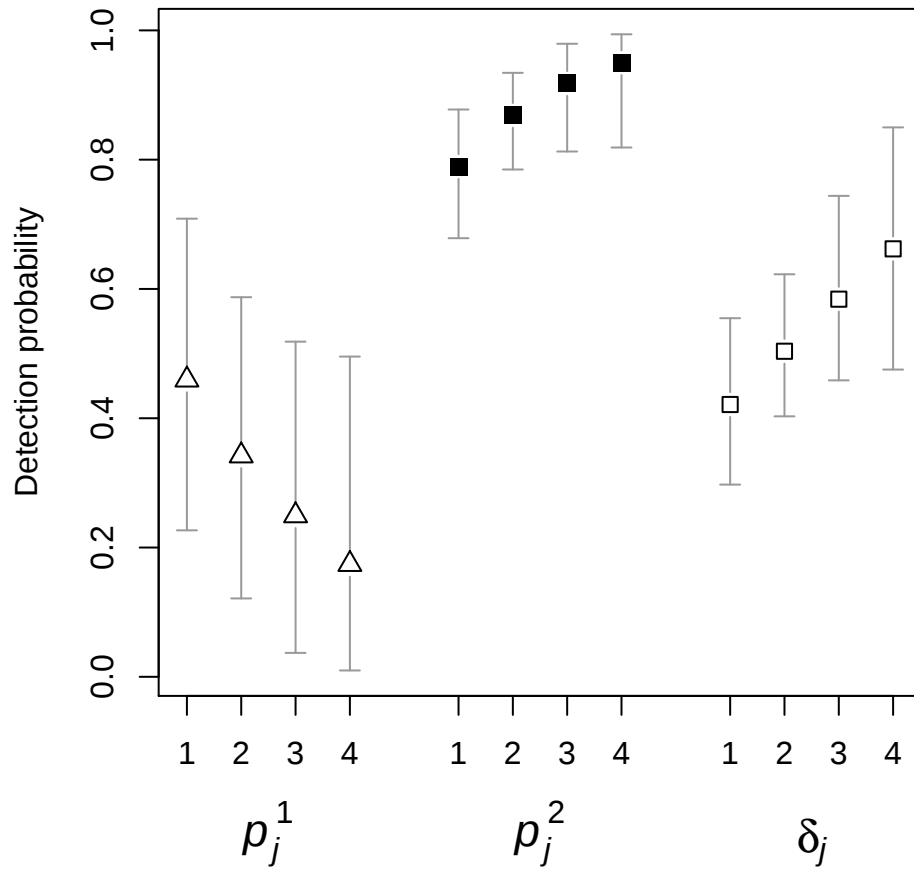


Figure 2.4. Model predicted mean probabilities of detection with 95% credible intervals over the 4 survey intervals. The probabilities are detection of occupancy given the site is occupied without nesting (p_j^1 , open triangles), detection of occupancy given the site is occupied with nesting (p_j^2 , filled squares), and detection of nesting given the site is occupied with nesting (δ_j , open squares).



CHAPTER 3

FACTORS AFFECTING WHITE-HEADED WOODPECKER (*PICOIDES ALBOLARVATUS*) REPRODUCTIVE SUCCESS IN MANAGED FORESTS WITH STRUCTURE RETENTION

Abstract

The importance of woodpeckers to forest bird communities and their sensitivity to forest management practices make them a suitable target for addressing conservation objectives in managed forests. Understanding the impact of management activities on woodpecker populations can be improved by examining how metrics of reproductive success relate to altered habitat conditions. We estimated nest survival and number of young fledged for white-headed woodpeckers (*Picoides albolarvatus*) located on private timberlands in northern California, USA from 2009–2010. We documented a high nest success rate (0.85, 95% credible interval: 0.59–0.96) and found that successful nests were most likely to produce ≥ 3 young. None of the habitat variables that were examined at multiple scales were able to describe variation in either metric of reproductive success. There was weak support for a date effect on number of young fledged, with more young fledged from nests that finished during the middle of the season. The high fecundity exhibited by woodpeckers in our study area suggests that the population may serve as a source. Current forest management practices appear to be providing habitat conditions that are conducive to the species' persistence in this region.

Keywords: Bayesian framework, California, fecundity, managed forests, nest survival, reproductive success, structure retention, white-headed woodpecker

1. Introduction

Woodpeckers are often regarded as indicators of forest ecosystem health and integrity due to their reliance on habitat features (e.g., large dead trees, or snags) most characteristic of old, unmanaged forests (Angelstam and Mikusinski, 1994; Drever *et al.*, 2008). In addition, the role of woodpeckers as ecosystem engineers and keystone species can influence the biodiversity of forest wildlife communities (Daily *et al.*, 1993; Jones *et al.*, 1994; Mikusinski *et al.*, 2001; Martin *et al.*, 2004; Virkkala, 2006). Woodpeckers require snags as substrate for foraging and nesting. They excavate cavities for rearing young and rarely reuse previous cavities, creating a valuable resource for secondary cavity-nesters (Martin and Eadie, 1999). In North America, secondary cavity-nesters rely almost exclusively on woodpeckers as their source for tree cavities (Cockle *et al.*, 2011). Forest management activities that remove large trees and snags are detrimental to many forest vertebrates, and cavity-nesting species are especially vulnerable due to nest-site limitation (Newton, 1994). Setting habitat targets that fulfill the resource requirements for woodpeckers has the potential to be a useful forest management strategy to address biodiversity conservation objectives (Drever and Martin, 2010).

The white-headed woodpecker (*Picoides albolarvatus*) is an omnivorous primary excavator associated with pine forests characterized by large trees and open canopies in western North America (Garrett *et al.*, 1996). This woodpecker requires moderately decayed snags for nesting substrate and large mature pine trees for foraging; it relies on pine seeds as a primary food source during the winter and possibly throughout the year (Ligon, 1973; Dixon, 1995). Recent studies of the white-headed woodpecker have emphasized habitat attributes affecting the nesting ecology of the species which may be

modified by forest management practices that include salvage logging in burned forests (Wightman *et al.*, 2010), fuel reduction in dry forests (Hollenbeck *et al.*, 2011), and methods to improve timber production (Kozma, 2009, 2011). These studies estimated nest survival as a function of biotic and abiotic factors, including habitat variables such as density of large snags and live trees. Additional information included habitat suitability models to predict nest locations (Wightman *et al.*, 2010; Hollenbeck *et al.*, 2011) and detailed nest demographic data (e.g., average clutch size, number of young fledged)(Kozma, 2009). This research has contributed much to our knowledge of white-headed woodpecker ecology, particularly for the regions (i.e., Oregon and Washington, USA) where the species is considered threatened by state and federal natural resource agencies due to population declines that have likely resulted from reductions in the amount of old-growth pine forests (Kozma, 2009). Unfortunately, only one field study exists on white-headed woodpeckers in the core of the species range in California (Raphael and White, 1984), where habitat selection and population ecology may differ compared to areas on the range periphery (Hardie and Hutchings, 2010).

Our objective was to examine factors influencing white-headed woodpecker reproductive success in managed forests of northern California. Previous research investigating the impact of structure retention practices on forest bird communities in the region discovered a high prevalence of white-headed woodpeckers nesting in recent clearcuts. We found the probability of nesting was significantly increased in harvest units with greater densities of retained snags, and estimated high probabilities of occupancy (0.98) and nesting (0.89) across harvest units in the study area (Chapter 2). Here we use nest monitoring data to estimate two components of reproductive success, the

probabilities of nest survival and number of young fledged. Nest survival alone does not properly quantify reproductive success, given that it represents one of several events necessary for an individual to contribute to recruitment in a population (Etterson *et al.*, 2011). For avian species that lay a single clutch during the breeding season, like most woodpeckers (Martin, 1993), the sequence of events defining fecundity involve successful pairing and nest construction, egg laying and incubation, rearing of young to independence, and post-fledging survival (Etterson *et al.*, 2011). Nests that survive to produce ≥ 1 young provide an opportunity for recruitment, and this opportunity increases with the number of young fledged. Therefore, quantifying the impacts of forest management on woodpecker populations can be improved through examination of multiple processes that affect recruitment. Our specific objectives were to 1) estimate reproductive parameters of white-headed woodpeckers in forests managed for timber production and 2) examine factors that influence these parameters, particularly habitat variables that are altered by forest management practices. We hypothesized that resource availability might influence nest survival but would likely explain more variation in the number of young fledged.

2. Methods

2.1. Study area

Our study was conducted on private industrial timberlands surrounded by the Shasta-Trinity National Forest east of Mt. Shasta in Siskiyou county, northern California (centered around 41°21'N, 121°50'W)(Figure 3.1). The area was covered by second- and third-growth, mixed-conifer forest that was historically dominated by ponderosa pine (*Pinus ponderosa*) and is now mostly white fir (*Abies concolor*). Selective logging and fire

suppression in the last century have altered the overstory composition similar to other dry forests of western North America (Hessburg *et al.*, 2005). Additional overstory species (in decreasing order of prevalence) included Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), California incense-cedar (*Calocedrus decurrens*) and sugar pine (*Pinus lambertiana*). Non-forested areas were typically chaparral vegetation composed primarily of manzanita (*Arctostaphylos spp.*). Elevations ranged from 1250–1950m, with true fir (*Abies spp.*) dominance generally increasing with elevation. Size classes of forest stands were variable: ~41% was comprised of mature stands with a quadratic mean diameter (QMD; diameter of tree representing average basal area) >60cm, ~36% contained younger stands with a QMD ranging 25–60cm, and the remaining ~20% of stands were evenly split among past harvests (QMD = 12–25cm), relatively recent harvests (QMD = 3–12cm) and new harvests (planted with seedlings)(U.S. Forest Service, 2007).

We selected all harvest units that were clearcut with retention between 3–6 yrs prior to 2009 in the study area (n=65). Recent harvests (<1 yr old) were not selected to avoid potential disturbance effects from harvesting and replanting activities. Harvest units had a mean area = 9ha (range = 4–15ha) and typically contained 1–6 patches (~0.1ha) of green-tree retention that were randomly dispersed throughout the unit, in addition to varying densities of snags that were retained during harvest (including stumps >1m tall). Slopes ranged from 0–100% (mean = 28%) and were variable across harvest units but mostly homogenous within harvest units, as part of forest planning. Mean monthly temperatures (at lower elevations) ranged from 2°C in January to 20°C in July; annual precipitation was 124cm with >75% falling as snow from November-March (National

Climatic Data Center, National Oceanic and Atmospheric Administration;
<http://www.ncdc.noaa.gov/>).

2.2. Nest searching and monitoring

We searched each harvest unit for white-headed woodpeckers with a passive survey that involved recording detections of individuals and using behavioral cues (e.g., individuals viewed carrying food or entering a snag cavity) to determine the presence of a cavity nest. Harvest units were searched systematically from June–July in 2009 and 2010 on days with good weather conditions (no rain or heavy wind). Harvest units that were not found to contain a nest were revisited every ~10 days with priority given to those sites where ≥ 1 adult white-headed woodpecker was detected.

Nests were monitored with a custom-built cavity-viewing camera system using methods similar to Huebner and Hurteau (2007). During each monitoring visit we recorded date, time, number of eggs or young and estimated nest age based on the size and feather development of nestlings. We attempted to visit each active nest every 3–4 days to accurately determine nest fate. Nests were considered successful if an empty nest was preceded by the observation of large nestlings that appeared close to fledging based on behavior (Martin and Geupel, 1993). Failure was assumed for all nests that were found empty at a date considered too early for fledging (according to estimated nest age) or when evidence indicated predation. Fledging date for successful nests was estimated as the midpoint between the dates of the last nest visit (when the cavity was found to be empty) and the visit prior. Initiation date for successful nests was estimated by assuming a total nesting period (egg-laying through fledging) of 40 days (Wightman *et al.*, 2010) and subtracting the total nesting period from the estimated fledging date. The number of

fledged young was estimated as the highest count of nestlings recorded after 80% completion of the nesting period for a given nest (Nappi and Drapeau, 2009); we chose this criterion to account for nests with a fledging period that spanned multiple days.

2.2. Model covariates

We included temporal and biotic factors as model covariates that might influence reproductive success. The temporal factors included ordinal date and year. We included a year effect due to higher winter snowfall and cooler spring temperatures in 2010, which resulted in a delayed onset of nesting. We did not include abiotic factors, such as maximum temperature and precipitation, which are sometimes hypothesized to influence nest survival (Wightman *et al.*, 2010; Saab *et al.*, 2011) because we predicted these variables would have little impact. Despite the cooler spring temperatures in 2010, maximum daily temperatures converged quickly between the years to become similar during our nesting observation period (June–July) and precipitation during that time was minimal and mostly invariant. Therefore, while weather conditions differed between the years prior to the nesting period, daily differences in weather during the nesting period were small and unlikely to explain much variation. Maximum daily temperatures were also highly correlated with date in both years ($r = 0.85$), and we were more interested in comparing the effects of covariates that could be incorporated into both metrics of reproductive success (i.e., daily survival rate as a function of date, and number of young fledged as a function of nest completion date).

The biotic factors included in the models were described by habitat variables measured at the levels of the nest site, harvest unit, and surrounding landscape. Field measurements were conducted at the completion of nest monitoring to avoid disturbing

active nests. We recorded species, height, dbh and decay class (Bull *et al.*, 1997) of nest snags, as well as the cavity entrance height and directional bearing. We estimated the live and dead tree basal area surrounding each nest site using variable-radius plots with a basal area factor 10 prism; this variable-radius method emphasizes larger trees. We measured snag density at each harvest unit by tallying all standing dead wood >12.7cm dbh and >1m in height, including snags <5m from the harvest unit boundary. Tall stumps were known to be used for cavity nests by white-headed woodpeckers (Milne and Hejl, 1989) and, thus, were included in the snag tallies. Harvest unit boundaries were determined within a geographic information system (GIS) by examining shapefiles of Timber Harvest Plans (THP; California Department of Forestry; <ftp://ftp.fire.ca.gov/forest/>) and 2 sets of 1-m resolution aerial photography from the National Agricultural Imagery Program (NAIP) collected in 2005 and 2009 (<http://datagateway.nrcs.usda.gov/>). We used the calculated harvest unit area to determine snag density for stems >25.4cm diameter, which represented the lower limit for white-headed woodpecker cavity nests observed in the field and in previous studies (Milne and Hejl, 1989; Kozma, 2009). We used a GIS to calculate the proportion of mature forest within a 1-km radius of all nest trees to estimate the availability of large trees for foraging; the 1-km radius represented the estimated home range of a white-headed woodpecker (Garrett *et al.*, 1996; Hollenbeck *et al.*, 2011). Mature forest was designated by areas containing trees with a QMD >60cm, as determined by the California Wildlife Habitat Relationships (CWHR) classification provided in the CALVEG geodatabase (U.S. Forest Service, 2007). We calculated mature forest proportion for both years separately due to timber harvesting that took place between the 2009 and 2010 field seasons. The locations of these new harvest units were mapped with a combination of the

THP shapefiles (indicating the areas with planned harvests) and 2010 Landsat Thematic Mapper imagery (<http://landsat.gsfc.nasa.gov/>) given that the most current NAIP photography was collected prior to the recent harvesting. The CALVEG geodatabase was then updated accordingly.

Our selection of model covariates describing habitat was reduced upon examination of the data to include only those factors that exhibited variation and had a biologically meaningful interpretation (Table 3.1). Basal areas of live trees, snags, and all stems >25.4cm dbh were low across nest sites, with 80%, 82%, and 64% of monitored nests having a basal area of 0 for each category, respectively. Snag tree species and decay class also exhibited little variation (84% of nests in true fir and 89% in moderately decayed snags); therefore, these attributes were not included in the modeling.

2.4. Statistical analysis

2.4.1. Nest survival

We modeled nest survival using a generalized linear modeling approach that estimates the probability of a nest surviving a specified time interval as a function of site- and time-specific covariates (Rotella *et al.*, 2004). The approach accounts for data structures that are typical of avian nest survival studies where entry of nests is staggered, nest visit intervals are unequal, and the exact date of nest success or failure is unknown (Dinsmore *et al.*, 2002). In the model specification, nest i survives from time t to $t + 1$ with a probability of ϕ_{it} , known as the daily survival rate (DSR) when the time interval is specified in days. The required information for each nest includes the first day the nest is discovered, the last day the nest is checked, the day prior to the last check, and the nest fate (success = 1, failure = 0). This information is used to construct an encounter history for

each nest and the estimation of ϕ_{it} is obtained by maximizing the likelihood of the product of the probabilities for the observed encounter histories (Dinsmore *et al.*, 2002). Relating individual covariates to the survival probability can be achieved with a logit link function. Following the notation of Royle and Dorazio (2008), we constructed a model of nest survival such that,

$$\text{logit}(\phi_{it}) = \beta_0 + \beta_{1yr}date_{it} + \beta_{2yr}date_{it}^2 + \beta_3nestht_i + \beta_4nestdbh_i + \beta_5snagdensity_i + \beta_6forest_i$$

where ϕ_{it} is the daily survival rate for nest i ; β_0 is the logit-transformed survival probability at average covariate values; β_{1yr} and β_{2yr} are year-specific coefficients for the linear and quadratic effects of date, respectively; and $\beta_3, \beta_4, \beta_5$ and β_6 are coefficients for the linear effects of nest height, nest tree dbh, snag density in the harvest unit, and proportion of mature forest surrounding the nest, respectively. The average probability of a nest surviving the entire nesting period is calculated by $\prod_{t=1}^m \phi_t$, where $m = 40$ for white-headed woodpeckers (Wightman *et al.*, 2010).

2.4.2. Number of young fledged

We modeled the number of young fledged from successful nests using an ordinal logistic regression which can handle count data that are underdispersed (i.e., variance < mean)(Agresti, 2002). While underdispersion of reproductive data should be a common occurrence for organisms with small clutch/brood sizes (<5) having a mean near the midpoint of the range, and has been reported for numerous avian species (Cohen, 1988), this issue appears to be rarely addressed in the literature where simple average sizes are reported and compared (*but see* Paradis *et al.*, 2000). Ordinal logistic regression estimates

the probabilities of an ordinal response y that can take $k = 1, 2, \dots, K$ categories where $\Pr(y = k) = \Pr(y > k - 1) - \Pr(y > k)$; cumulative probabilities are related to covariates with a logit link function (Gelman and Hill, 2007). The logit-linear models have different intercepts but the same beta coefficients for covariates that are hypothesized to affect the cumulative probabilities, $\Pr(y \leq k)$. Thus, the model makes the proportional odds assumption – the effects of covariates are the same across different cumulative logits (e.g., the logistic regression comparing $k \leq 1$ to $k > 1$ is the same as that for comparing $k \leq 2$ to $k > 2$) (Agresti, 2002). Our model for number of young fledged was specified similarly to the nest survival model such that,

$$\begin{aligned} \text{logit}\left(Q_i^{[k]}\right) &= \lambda^{[k]} - \mu_i \\ \mu_i &= \beta_0 + \beta_{1yr} \text{comp.date}_{it} + \beta_{2yr} \text{comp.date}_{it}^2 + \beta_3 \text{nestht}_i + \\ &\quad \beta_4 \text{nestdbh}_i + \beta_5 \text{snagdensity}_i + \beta_6 \text{forest}_i \end{aligned}$$

where $Q_i^{[k]}$ is the cumulative probability that number of young y is $\leq k$ at nest i , with $Q_i^{[K]} = 1$ (i.e., the probability that y is $\leq$ the maximum observed number of young K is 1); $\lambda^{[k]}$ is an ordered cutoff parameter for the ordinal responses satisfying $\lambda^{[1]} < \lambda^{[2]} < \dots < \lambda^{[K-1]}$; and μ_i represents the summation of covariate effects on the categorical probability distribution, with an intercept β_0 , year-specific parameters, β_{1yr} and β_{2yr} , for the linear and quadratic effects of nest completion date, and additional parameters $\beta_3, \beta_4, \beta_5$, and β_6 for the effects of site-specific habitat covariates, as explained in the nest survival model. With this model specification, a positive value for a β coefficient increases the expected number of young for a given nest. This allows the interpretation of covariate

effects to remain consistent between the models for daily survival rate and number of young fledged.

2.4.3. Model parameter estimation

We used a Bayesian approach with Markov chain Monte Carlo (MCMC) to estimate model parameters for both survival and number of young fledged in WinBUGS (Spiegelhalter *et al.*, 2003). WinBUGS uses Gibbs sampling (Geman and Geman, 1984) to draw samples from the joint probability distribution of each specified model and estimate posterior distributions for each model parameter. The posterior distributions are summarized by means and credible intervals, which are the Bayesian analogs to confidence intervals. We specified the models and formatted the data inputs using the R2WinBUGS package (Sturtz *et al.*, 2005) in R (R Development Core Team 2011). All covariates were standardized to have a mean of 0 and unit variance of 1 to allow comparison of effect sizes. Non-informative priors were specified for all parameters in the logit-linear models, with a uniform distribution from 0 to 1 for the intercepts and diffuse normal distributions for parameters describing covariate effects (mean = 0, variance = 100). Diffuse normal distributions were also specified for the $\lambda^{[k]}$ cutoff parameters, with values restricted to satisfy the ordering. We examined the posterior distributions for each set of model parameters after running 3 chains of 100,000 iterations and discarding the first 50,000 iterations. Posterior chains were thinned by 25 to reduce autocorrelation, resulting in 6,000 values forming the posterior distribution for each parameter. Model convergence was assessed by examination of trace plots and the scale reduction factor, or R-hat statistic. Convergence was assumed when the R-hat statistic was <1.1 for all model parameters (Gelman and Hill, 2007). We assessed the significance of regression coefficients based on

whether the estimated credible intervals overlapped zero; strong support for a covariate effect was indicated when the 95% CRI did not overlap zero, while weak support was indicated when the 90% CRI did not overlap zero. WinBUGS code for model specification is presented in the Appendix (A.3, A.4).

3. Results

We monitored 89 nesting attempts by white-headed woodpeckers from 2009–2010, nearly evenly split between the years with 45 in 2009 and 44 in 2010. Nests were well distributed across the study area: of the 65 harvest units searched each year, 42 were found to have ≥ 1 nest in 2009 and 41 in 2010. Nest occupancy shifted among harvest units between the years, as 53 harvest units had ≥ 1 nest during the course of the study, and 30 harvest units had ≥ 1 nest in both years. A total of 3 harvest units in each year were found to have 2 nests, with 2 harvest units having multiple nests each year.

We observed low nest failure in both years, with only 6 of the 89 nesting attempts failing to produce ≥ 1 young. All 6 nest failures were assumed to be the result of depredation given lack of evidence otherwise (Wightman *et al.*, 2010), and 3 nest failures were attributed to black bear (*Ursus americanus*) based on observations of fallen snags with cavity nests torn open (we frequently observed bears both in and around harvest units during the study). The nesting stage upon first discovery was incubation for 22% of nests and nestling for the remaining 78% across the 2 years. The average completion dates for successful nests were estimated at 5 July in 2009 (range: 24 June–24 July) and 13 July in 2010 (range: 28 June–2 August). The number of young fledged from successful nests was similar across years (Table 3.2) and ranged from 1–5, with an overall average count of

2.94 fledglings (SE = 0.10). As expected, this distribution could not be properly described by a Poisson distribution due to severe underdispersion, given that 94% of nests fledged between 2–4 young and the variance (0.84) was much lower than the mean (Table 3.2).

The models for daily survival and number of young fledged indicated that none of the temporal or biotic habitat variables had strong support for an effect on either metric of reproductive success (Table 3.3). The daily survival rate estimated at average covariate values was 0.996 (95% CRI: 0.987–0.999), resulting in a period survival rate (assuming a 40-day nesting period) of 0.85 (95% CRI: 0.59–0.96). We found weak support for a quadratic date effect on daily survival rate with survival decreasing during the middle portion of the nesting period (Figure 3.2), but the estimate was imprecise. Likewise, we found weak support for a quadratic effect of nest completion date on the number of young fledged: nests that fledged in the middle of the season had a marginally higher expected number of young (Figure 3.3). Support for the quadratic date effect in each model was higher for data from 2010 than that for 2009 (Table 3.3; Figures 3.2–3.3), though the uncertainty makes it difficult to determine whether the annual variation was actually significant. At average values for covariates, the probability that number of young fledged would be ≥ 3 was 0.79 (95% CRI: 0.62–0.90).

4. Discussion

Reproductive success is a fundamental element of wildlife population dynamics, and management strategies which aim to assist species persistence should address the environmental factors that drive reproductive success. Reproductive success was high for white-headed woodpeckers nesting on industrial timberlands in northern California during

2009 and 2010. We estimated high daily survival rates and subsequently high nest success (0.85), with the majority of successful nests likely to fledge ≥ 3 young. Our nest success estimate is similar to those for white-headed woodpeckers in unburned managed forests of central Washington (0.84; Kozma, 2009) and higher than those in burned (0.76; Wightman *et al.*, 2010) and unburned (0.39; Hollenbeck *et al.*, 2011) forests of central Oregon. Kozma (2009) described white-headed woodpecker nesting demographics and found successful nests averaged 2.54 young/nest, which was lower than sympatric hairy woodpeckers (*Picoides villosus*); this finding was used to hypothesize that white-headed woodpeckers might be nesting in suboptimal habitat on managed forests in Washington. Nappi and Drapeau (2009) calculated source-sink status for black-backed woodpeckers (*Picoides arcticus*) using average adult and juvenile survival estimates from the literature for *Picoides* woodpeckers and suggested that nest productivity (nest success $\times$ young/nest) needed to be >2 for the population to serve as a source, under intermediate to high adult and juvenile survival. Assuming intermediate survival rates for adults (0.65) and juveniles (0.33) and using the logic from Nappi and Drapeau (2009), nest productivity in our study area was ~ 2.5 , indicating that this population of white-headed woodpeckers may serve as a source. Our study suggests that current forest management practices in northern California are providing habitat conditions which facilitate white-headed woodpecker population persistence in this region.

The few nest failures in our study made it difficult to assess factors influencing nest survival, especially when considering that 3 of the 6 failures were attributed to a large and mobile generalist predator (i.e., black bear). The susceptibility of cavity nest depredation to black bears is going to be more a function of snag condition than habitat, given that

heavily decayed snags can be easily pushed over and ripped apart. White-headed woodpeckers are a relatively weak primary excavator (Garrett *et al.*, 1996), so the majority of snags that serve as cavity nests are likely to be at least moderately decayed. Wightman *et al.* (2010) found similarly low nest depredation rates for white-headed woodpeckers which they attributed to the lack of live tree density and low cover for small mammalian predators (e.g., squirrels) that are often responsible for cavity nest depredation (Martin, 1995). The nest sites we observed were also characterized by a lack of live tree cover due to their location within clearcut harvest units. In this context, the removal of tree cover resulting from timber harvest likely has a similar effect to that from wildfire, though other differences between these two disturbance events have important implications for forest ecosystems (Lindenmayer and Noss, 2006). Kozma and Kroll (*in press*) found that shrub cover decreased nest survival of white-headed woodpeckers and hypothesized that woodpeckers had a reduced ability to defend nests against small mammalian predators in areas with high shrub cover. The nests observed in our study had a low average cavity height (3.1m), which is typical of the species (Milne and Hejl, 1989); thus, the lack of shrub cover in harvest units intensively managed for timber production may provide optimal conditions by increasing nest defense capabilities.

Our hypothesis that the variation in number of young fledged could be explained by resource availability as quantified by habitat attributes in and around nest sites was not supported by the data. White-headed woodpeckers rely on various insects for foraging during the breeding season that likely become more available as summer temperatures increase (Elchuk and Wiebe, 2003) which may explain the later timing in their nest initiation compared to sympatric species like hairy woodpeckers (Kozma, 2009). Relative

temperatures are typically higher in clearcut harvest units which can increase insect abundance and has been shown to increase woodpecker abundance in stands with tree retention (Edworthy *et al.*, 2011). Thus, food resources across the harvest units in our study area may not have been limiting during the breeding season. Woodpeckers have generally low clutch sizes because of stable food resources that do not confer advantages to fluctuations in reproductive investment from year to year, which is more typical of migratory species that exploit stochastic food resources (Wiebe *et al.*, 2006). While strong excavating species (e.g., hairy woodpeckers) often have access to a stable food resource by drilling for bark burrowing beetles throughout the year, the use of pine seeds by white-headed woodpeckers may result in the same advantages in regions where pine species are a common/dominant overstory tree. Landscapes that contain a mosaic of open and closed canopy forest with presence of mature pine may therefore provide both foraging resources (i.e., insects and pine seeds) required by white-headed woodpeckers (Wightman *et al.*, 2010). The high, stable fecundity exhibited in our study area suggests that white-headed woodpeckers were occupying high quality habitat.

5. Management implications

Forest management on private industrial timberlands in the Pacific Northwest is characterized by structure retention policies which mandate that minimum densities of snags and live trees are left behind during harvesting operations. In northern California, these retention policies, in addition to restrictions on harvest unit size, appear to provide nest site conditions for white-headed woodpeckers that support relatively high nest success and fecundity. We recommend that forest managers retain every available snag

that can be safely left standing during harvest operations to maintain the availability of nest sites for woodpeckers. Stands with low snag densities should be supplemented with high-cut stumps, which have been shown to provide a suitable nesting substrate for white-headed woodpeckers. We also recommend that live tree retention should include mature pines (e.g., ponderosa and sugar) where forest composition permits, given the importance of this food resource for winter survival of white-headed woodpeckers. Uncertainty exists regarding the temporal dynamics of white-headed woodpecker occupancy in recent harvest units, specifically the duration over which stands with snag retention can adequately provide nesting opportunities. Harvest units may provide a relatively small window of opportunity given the change in habitat conditions due to snag decay and falling, which reduces nest site availability, and growth of regenerating trees, which increases cover for nest predators. Future research should examine how current landscape-level forest planning influences the temporal and spatial distribution of nesting habitat for white-headed woodpeckers.

Table 3.1. Summary of potential model covariates describing habitat collected at multiple scales for white-headed woodpecker nests from 2009–2010 in northern California, USA. Habitat variables were measured at the level of the nest tree, nest site, stand, and landscape for all monitored nests (n=89). Variables in bold were selected for use in the models of reproductive metrics.

Variable	Mean (SD)	Min	Max
<i>Nest tree level</i>			
Tree diameter (cm)	53.0 (24.2)	17.5	152.4
Nest height (m)	3.1 (1.9)	0.9	11.0
<i>Nest site level</i>			
Basal area (m ² /ha) ^a			
All stems	2.3 (4.8)	0	25.3
Live trees	1.7 (4.7)	0	25.3
Snags	0.6 (1.4)	0	6.9
<i>Stand level</i>			
Snag density (#/ha)	2.5 (1.4)	0.3	6.1
<i>Landscape level</i>			
Mature forest (%)^b	41 (14)	9	71

^a For trees >25.4cm dbh.

^b Within 1-km radius of nest tree.

Table 3.2. Count of white-headed woodpecker nests that successfully fledged young during 2009 and 2010 on private timberlands of northern California, USA. Mean and standard error (SE) for number of young fledged are also presented for each year.

Year	Number of young fledged					Mean (SE)
	1	2	3	4	5	
2009	2	15	15	10	1	2.84 (0.14)
2010	1	11	14	13	1	3.05 (0.14)

Table 3.3. Posterior summaries for model parameters (means, standard deviations [SD], and 95% credible intervals [0.025 and 0.975]) from the logit linear models for nest survival and number of young fledged. Temporal covariates were year-specific linear and quadratic effects of ordinal date for daily nest survival ($date_i, date_i^2$) and nest completion date for number of young ($comp.date_i, comp.date_i^2$). Habitat covariates were nest height ($nestht_i$), nest tree diameter ($nestdbh_i$), snag density in the harvest unit ($snagdensity_i$), and mature forest proportion in a 1-km radius surrounding the nest ($forest_i$).

Table 3.3 (cont'd)

Parameter	Mean	SD	0.025	0.975
Nest survival				
β_0	5.543	0.713	4.340	7.109
$\beta_{1,1}$ (<i>date_i</i> 2009)	-0.221	1.729	-3.657	3.320
$\beta_{1,2}$ (<i>date_i</i> 2010)	-2.621	1.419	-5.737	-0.217
$\beta_{2,1}$ (<i>date_i²</i> 2009)	1.981	1.715	-0.377	6.137
$\beta_{2,2}$ (<i>date_i²</i> 2010)	1.396	0.986	-0.060	3.657
β_3 (<i>nestht_i</i>)	-0.438	0.441	-1.366	0.392
β_4 (<i>nestdbh_i</i>)	-0.291	0.396	-1.061	0.479
β_5 (<i>snagdensity_i</i>)	0.715	0.480	-0.236	1.653
β_6 (<i>forest_i</i>)	-0.377	0.498	-1.439	0.548
Number of young fledged				
β_0	0.073	1.711	-3.355	3.772
$\beta_{1,1}$ (<i>comp.date_i</i> 2009)	0.622	0.560	-0.432	1.777
$\beta_{1,2}$ (<i>comp.date_i</i> 2010)	-0.053	0.311	-0.662	0.559
$\beta_{2,1}$ (<i>comp.date_i²</i> 2009)	-0.321	0.406	-1.127	0.473
$\beta_{2,2}$ (<i>comp.date_i²</i> 2010)	-0.357	0.217	-0.797	0.062
β_3 (<i>nestht_i</i>)	-0.048	0.226	-0.496	0.400
β_4 (<i>nestdbh_i</i>)	0.041	0.221	-0.394	0.473
β_5 (<i>snagdensity_i</i>)	-0.055	0.292	-0.623	0.518
β_6 (<i>forest_i</i>)	-0.019	0.218	-0.435	0.408

Figure 3.1. Harvest units selected to study white-headed woodpecker reproductive success from 2009–2010 near Mt. Shasta, California, USA.

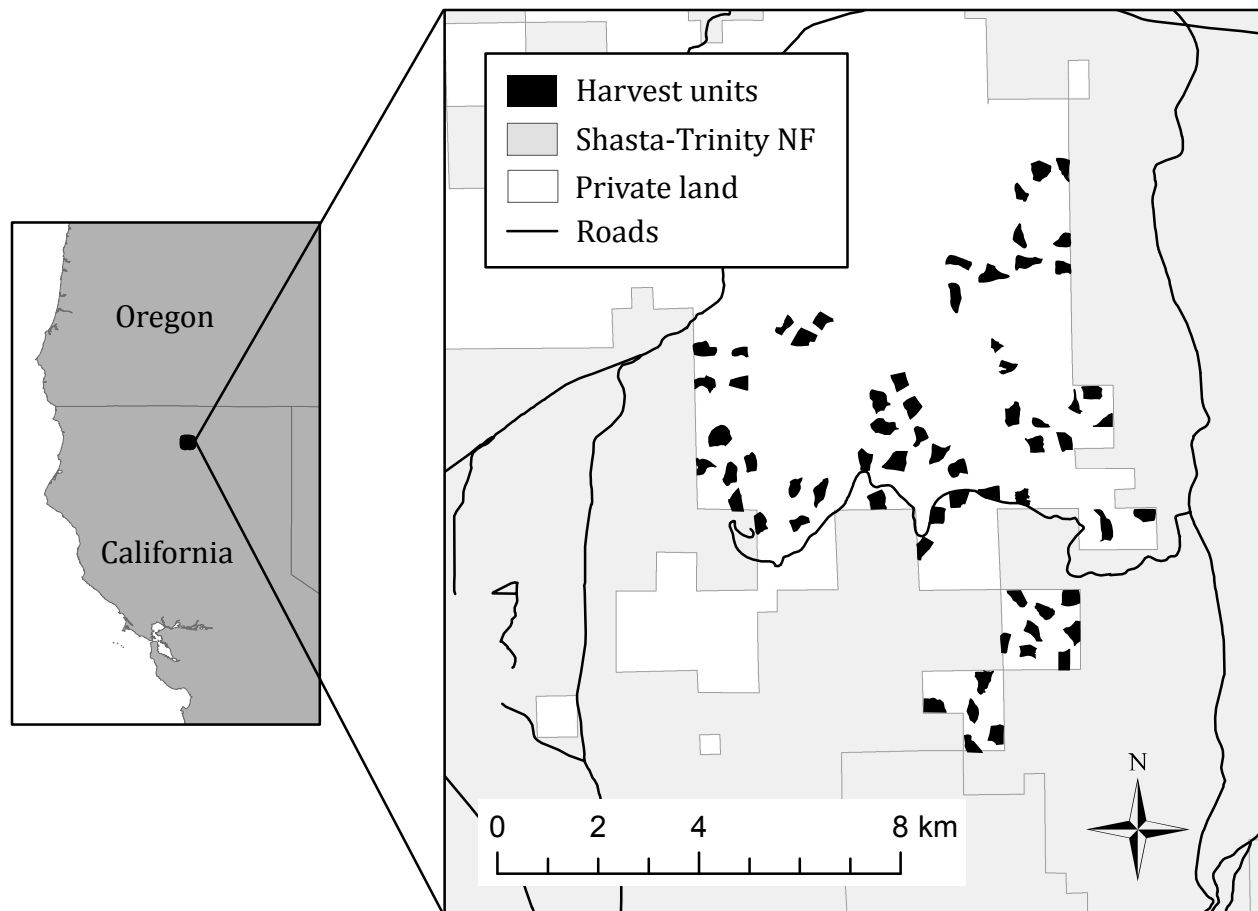


Figure 3.2. Predicted relationship between daily nest survival and ordinal date for white-headed woodpeckers during 2009 and 2010 in northern California, USA. Lines represent mean probabilities (solid) and 90% credible intervals (dashed).

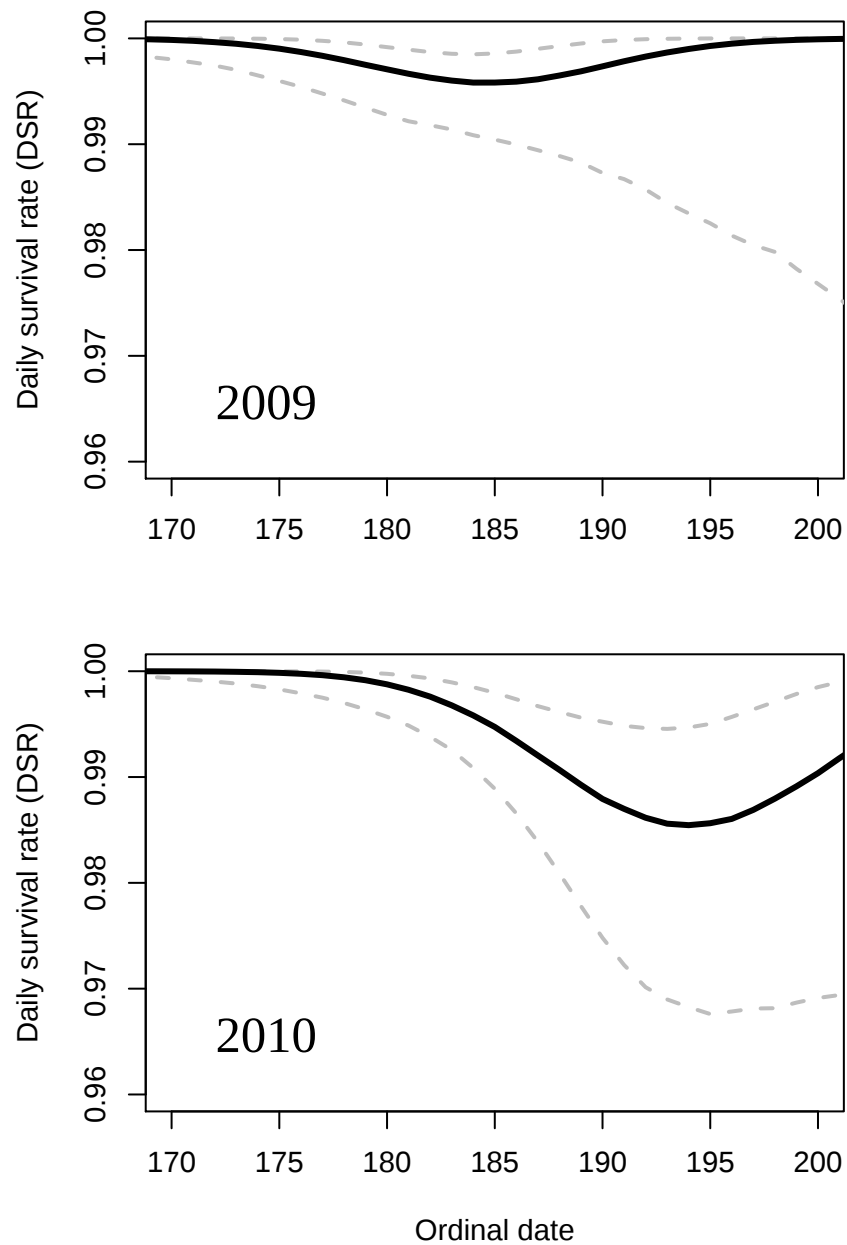
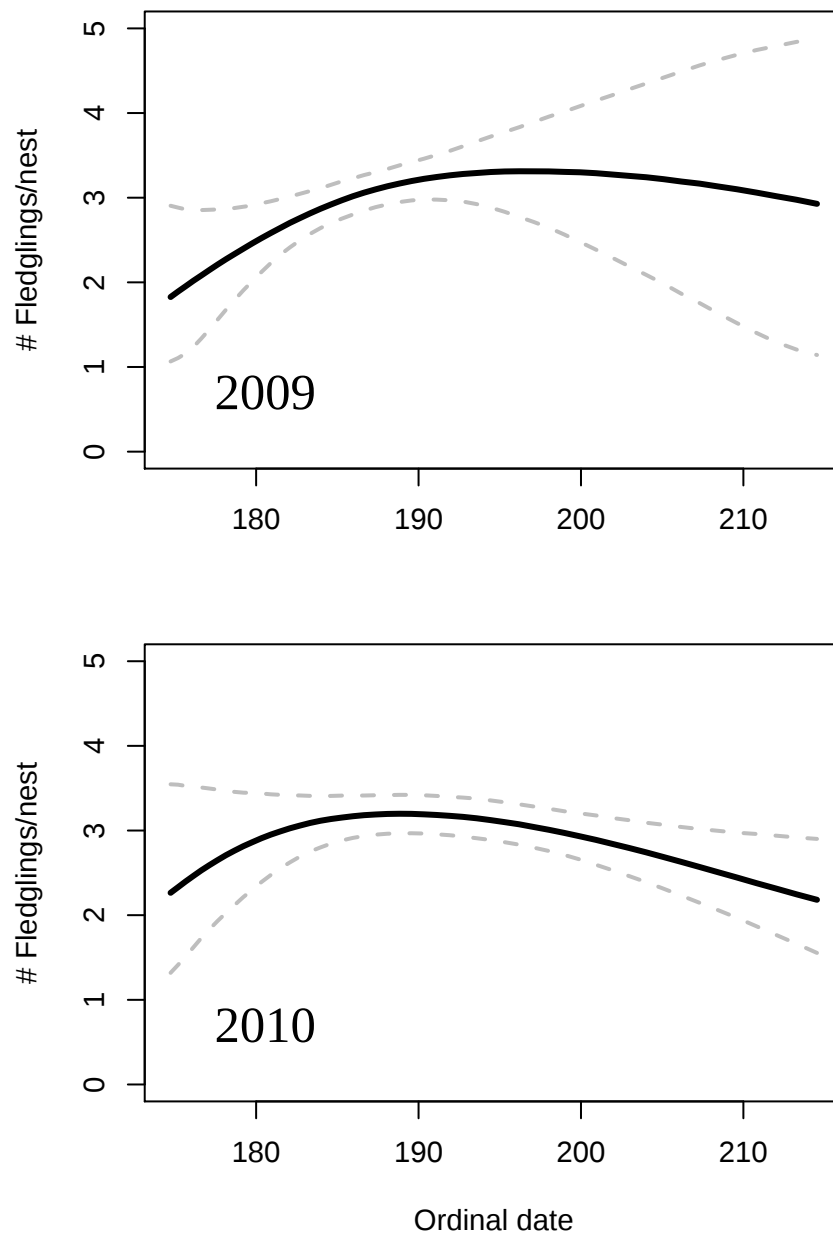


Figure 3.3. Predicted relationship between expected number of young fledged and ordinal date of nest completion for white-headed woodpeckers during 2009 and 2010 in northern California, USA. Lines represent mean probabilities (solid) and 90% credible intervals (dashed).



APPENDIX

APPENDIX A

Appendix A contains the WinBUGS code for all models in chapters 1–3. The code is annotated to provide general descriptions of model components. The model specifications are consistent with the formatting in WinBUGS. WinBUGS requires that normal distributions be specified in terms of precision (inverse variance) instead of standard deviation; precision is indicated by τ . Greek symbols from model specifications in the text are typically spelled out in the model code (e.g., ψ = psi, μ = mu). Index letters in the code are consistent with those in the text, though ordering is sometimes changed for looping purposes.

Note that data are required for these models to run in WinBUGS and are not provided here. The names of all data types (vectors, matrices, lists) required by each model are indicated at the end of the code.

Appendix A.1. WinBUGS code for community occupancy model (chapter 1)

```
model{
# Define prior distributions for community-level model parameters
# Priors defined separately, where appropriate, for the following:
#       1) FOREST and OPEN species (f)
#       2) study area (h)
#       3) year (t)

# Occurrence (u) probabilities in year 1
for (f in 1:2){
  for (h in 1:4){
    u.prob[f,h] ~ dunif(0,1)
    mu.u[f,h] <- logit(u.prob[f,h])
    tau.u[f,h] ~ dgamma(0.1,0.1)
  }
}

# Detection (v) probabilities
for (f in 1:2){
  for (h in 1:4){
```

```

    for (t in 1:2){
      v.prob[f,h,t] ~ dunif(0,1)
      mu.v[f,h,t] <- logit(v.prob[f,h,t])
      tau.v[f,h,t] ~ dgamma(0.1,0.1)
    }}

# Survival (phi) probabilities
for (f in 1:2){
  for (h in 1:4){
    phi.prob[f,h] ~ dunif(0,1)
    mu.phi[f,h] <- logit(phi.prob[f,h])
    tau.phi[f,h] ~ dgamma(0.1,0.1)
  }}

# Colonization (gamma) probabilities
for (f in 1:2){
  for (h in 1:4){
    gamma.prob[f,h] ~ dunif(0,1)
    mu.gamma[f,h] <- logit(gamma.prob[f,h])
    tau.gamma[f,h] ~ dgamma(0.1,0.1)
  }}

# Parameters for detection covariates (no separate distribution for
  FOREST vs. OPEN)
mu.a1 ~ dnorm(0, 0.001)
mu.a2 ~ dnorm(0, 0.001)
mu.a3 ~ dnorm(0, 0.001)
tau.a1 ~ dgamma(0.1,0.1)
tau.a2 ~ dgamma(0.1,0.1)
tau.a3 ~ dgamma(0.1,0.1)

# Parameters for the occupancy covariates
for (f in 1:2){
  mu.b1[f] ~ dnorm(0, 0.001)
  mu.b2[f] ~ dnorm(0, 0.001)
  mu.b3[f] ~ dnorm(0, 0.001)
  mu.b4[f] ~ dnorm(0, 0.001)
  tau.b1[f] ~ dgamma(0.1,0.1)
  tau.b2[f] ~ dgamma(0.1,0.1)
  tau.b3[f] ~ dgamma(0.1,0.1)
  tau.b4[f] ~ dgamma(0.1,0.1)
}

#Create priors for species i from the community level prior
distributions.
for (i in 1:n) {
  for (h in 1:4){
    u[i,h] ~ dnorm(mu.u[FD[i],h], tau.u[FD[i],h])
    v[i,h,1] ~ dnorm(mu.v[FD[i],h,t], tau.v[FD[i],h,t])
    v[i,h,2] ~ dnorm(mu.v[FD[i],h,t], tau.v[FD[i],h,t])
    phi[i,h] ~ dnorm(mu.phi[FD[i],h], tau.phi[FD[i],h])
    gamma[i,h] ~ dnorm(mu.gamma[FD[i],h], tau.gamma[FD[i],h])
  }
}

```

```

}
a1[i] ~ dnorm(mu.a1, tau.a1)
a2[i] ~ dnorm(mu.a2, tau.a2)
a3[i] ~ dnorm(mu.a3, tau.a3)

b1[i] ~ dnorm(mu.b1[FD[i]], tau.b1[FD[i]])
b2[i] ~ dnorm(mu.b2[FD[i]], tau.b2[FD[i]])
b3[i] ~ dnorm(mu.b3[FD[i]], tau.b3[FD[i]])
b4[i] ~ dnorm(mu.b4[FD[i]], tau.b4[FD[i]])

#Estimate the Z matrix (true occurrence for species i at site j)
for (j in 1:J) {
  # occupancy in year 1
  logit(psi[j,i,1]) <- u[i,studyarea[j]] + b1[i]*trees[j] +
    b2[i]*trees[j]*trees[j] + b3[i]*dist[j] + b4[i]*dist[j]*dist[j]
  Z[j,i,1] ~ dbern(psi[j,i,1])

  # occupancy in year 2
  logit(psi[j,i,2]) <- phi[i,studyarea[j]]*Z[j,i,1] +
    gamma[i,studyarea[j]]*(1-Z[j,i,1]) + b1[i]*trees[j] +
    b2[i]*trees[j]*trees[j] + b3[i]*dist[j] + b4[i]*dist[j]*dist[j]
  Z[j,i,2] ~ dbern(mu.pi[j,i,1])

#Model detections at site j and survey period k in year t.
for (t in 1:2) {
  for (k in 1:K) {
    logit(p[j,k,i,t]) <- v[i,h,t] + a1[i]*date[j,t] +
      a2[i]*date[j,t]*date[j,t] + a3[i]*pdet[j,k,i,t]
    mu.p[j,k,i,t] <- p[j,k,i,t]*Z[j,i,t]
    y[j,k,i,t] ~ dbern(mu.p[j,k,i,t])
  }}}

#Calculate point level richness estimates for the whole community,
  FOREST, and OPEN species.
for(t in 1:2) {
  for(j in 1:J) {
    N[j,t]<- sum(Z[j,1:n,t])
    N.forest[j,t]<- inprod(Z[j,1:n,t],forest[1:n])
    N.open[j,t]<- inprod(Z[j,1:n,t],open[1:n])
  }}

} #end model

#Data:
#   y = detection array for site j, survey k, species i, year t
#   n = number of species
#   K = number of surveys
#   studyarea = vector of study area codes (1-4) for each site j
#   FD = indicator of habitat group (1 or 2)

```

```
# date = matrix of ordinal dates for site j in year t
# pdet = array indicating previous detection
# trees = vector of tree counts for each site j
# dist = vector of edge distances for each site j
# forest = vector of dummy variable for FOREST species
# open = vector of dummy variable for OPEN species
```

Appendix A.2. WinBUGS code for multistate occupancy model (chapter 2)

```
model{
# state 1 = unoccupied, state 2 = occupied, state 3 = occupied w/ nest
for (i in 1:N){
  state[i,1] <- 1-psi1[i]          #state 1
  state[i,2] <- psi1[i]*(1-psi2[i]) #state 2
  state[i,3] <- psi1[i]*psi2[i]    #state 3

  States[i] ~ dcat(state[i,])

#logit occupancy model for occupied (state = 2)
  logit(psi1[i]) <- b10 + b11*snags[i] + b12*forest[i] + b13[i]
#logit occupancy model for occupied w/ nest (state = 3)
  logit(psi2[i]) <- b20 + b21*snags[i] + b22*forest[i] + b23[i]
#Mean of spatial random effects
  Zero[i] <- 0

  for (j in 1:J) {
    p[i,1,j,1] <- 1                # Pr(detect state1 | state1)
    p[i,1,j,2] <- 0                # Pr(detect state2 | state1)
    p[i,1,j,3] <- 0                # Pr(detect state3 | state1)

    p[i,2,j,1] <- 1-p1[i,j]        # Pr(detect state1 | state2)
    p[i,2,j,2] <- p1[i,j]          # Pr(detect state2 | state2)
    p[i,2,j,3] <- 0                # Pr(detect state3 | state2)

    p[i,3,j,1] <- 1-p2[i,j]        # Pr(detect state1 | state3)
    p[i,3,j,2] <- p2[i,j]*(1-d[i,j]) # Pr(detect state2 | state3)
    p[i,3,j,3] <- p2[i,j]*(d[i,j])  # Pr(detect state3 | state3)

    logit(p1[i,j]) <- a10 + a11*j
    logit(p2[i,j]) <- a20 + a21*j
    logit(d[i,j]) <- a30 + a31*j

    y[i,j] ~ dcat(p[i,States[i],j,])
  }
}}
```

```

#Priors for spatial random effects
b13[1:N] ~ spatial.exp(Zero[1:N],standX[],standY[], tau.sp[1],
                        alpha[1], 1)
b23[1:N] ~ spatial.exp(Zero[1:N],standX[],standY[], tau.sp[2],
                        alpha[2], 1)

for (w in 1:2){
  alpha[w] ~ dunif(1,30)
  upsiion[w] ~ dunif(0.1,3)
  tau.ups[w] <- pow(upsilon[w], -2)
  sigma[w] ~ djl.dnorm.trunc(0,tau.ups[w],0.5,2)
  tau.sp[w] <- pow(sigma[w], -2)
}

#Priors for other model parameters
a10.prob ~ dunif(0,1)
a20.prob ~ dunif(0,1)
a30.prob ~ dunif(0,1)
b10.prob ~ dunif(0,1)
b20.prob ~ dunif(0,1)

a10 <- logit(b10.prob)
a20 <- logit(b20.prob)
a30 <- logit(b30.prob)
b10 <- logit(a10.prob)
b20 <- logit(a20.prob)

a11 ~ dnorm(0, 0.001)
a21 ~ dnorm(0, 0.001)
a31 ~ dnorm(0, 0.001)
b11 ~ dnorm(0, 0.001)
b12 ~ dnorm(0, 0.001)
b21 ~ dnorm(0, 0.001)
b22 ~ dnorm(0, 0.001)

} #end model

#Data:
#   y = observed state at site i during survey j
#   N = number of sites
#   J = number of surveys
#   snags = snag density at site j
#   forest = proportion mature forest within 1-km radius of site j
#   standX = x coordinate for site j
#   standY = y coordinate for site j

```

Appendix A.3. WinBUGS code for nest survival model (chapter 3)

```
model {  
  
  for(i in 1:N){  
    for(t in (first[i]+1):last[i]){  
      logit(phi[i,t])<- b0 + b1[year[i]]*date[t] +  
        b2[year[i]]*date[t]*date[t] + b3*nestht[i] + b4*nestdbh[i] +  
        b5*snagdensity[stand.id[i]] + b6*forest[i]  
  
      mu[i,t]<-phi[i,t]*y[i,t-1]  
      y[i,t]~dbern(mu[i,t])  
    }  
  }  
  
  #Priors for logit models  
  b0.prob ~ dunif(0,1)  
  b0 <- logit(b0.prob)  
  #Different prior for each year  
  for (yr in 1:2){  
    b1[yr]~dnorm(0,0.001)  
    b2[yr]~dnorm(0,0.001)  
  }  
  b3 ~ dnorm(0,0.001)  
  b4 ~ dnorm(0,0.001)  
  b5 ~ dnorm(0,0.001)  
  b6 ~ dnorm(0,0.001)  
  
} #end model  
  
#Data:  
  
#   y = status (0=failed,1=active,NA=unknown) of nest i during time t  
#   N = number of nests  
#   first = first time period t that nest i was discovered  
#   last = last time period t nest i was observed to be active (y=1)  
#   year = year that nest i was observed (1 or 2)  
#   date = ordinal date of time period t  
#   nestht = cavity height of nest i  
#   nestdbh = diameter of snag in which nest i occurred  
#   stand.id = harvest unit within which nest i occurred  
#   snagdensity = density of snags in harvest unit for nest i  
#   forest = proportion of mature forest in 1-km radius around nest i
```

Appendix A.4. WinBUGS code for offspring model (chapter 3)

```
model {

for (i in 1:N){
  y[i] ~ dcat(P[i,])
  #Probability for each observed number of offspring (1-5)
  P[i,1] <- Q[i,1]
  P[i,2] <- Q[i,2] - Q[i,1]
  P[i,3] <- Q[i,3] - Q[i,2]
  P[i,4] <- Q[i,4] - Q[i,3]
  P[i,5] <- 1 - Q[i,4]
  for (j in 1:4){
    logit(Q[i,j]) <- lambda[j] - mu[i]
  }
  mu[i] <- b0 + b1[year[i]]*date[t] + b2[year[i]]*date[t]*date[t] +
    b3*nestht[i] + b4*nestdbh[i] + b5*snagdensity[stand.id[i]] +
    b6*forest[i]
}

# Ordered cut points for underlying continuous latent variable
# Restrict the priors so that lambda[k] < lambda[k+1]
lambda[1] ~ dnorm(0, 0.001)I(-20,lambda[2])
lambda[2] ~ dnorm(0, 0.001)I(lambda[1],lambda[3])
lambda[3] ~ dnorm(0, 0.001)I(lambda[2],lambda[4])
lambda[4] ~ dnorm(0, 0.001)I(lambda[3],20)

#Priors for logit models
b0.prob ~ dunif(0,1)
b0 <- logit(b0.prob)
#Different prior for each year
for (yr in 1:2){
  b1[yr]~dnorm(0,0.001)
  b2[yr]~dnorm(0,0.001)
}
b3 ~ dnorm(0,0.001)
b4 ~ dnorm(0,0.001)
b5 ~ dnorm(0,0.001)
b6 ~ dnorm(0,0.001)

} #end model

#Data:
#   y = number of young fledged by nest i
#   N = number of nests
#   year = year that nest i was observed (1 or 2)
#   date = estimated ordinal date that nest i fledged
#   nestht = cavity height of nest i
```

```
# nestdbh = diameter of snag in which nest i occurred
# stand.id = harvest unit in which nest i occurred
# snagdensity = density of snags in harvest unit for nest i
# forest = proportion of mature forest in 1-km radius around nest i
```

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