

AVIAN COMMUNITY RESPONSE TO A
MOUNTAIN PINE BEETLE EPIDEMIC

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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ABSTRACT

Recent epidemics of mountain pine beetles (*Dendroctonus ponderosae*) will fundamentally alter forests of the Intermountain West, impacting management decisions related to fire, logging, and wildlife conservation. We evaluated effects of a recent mountain pine beetle epidemic on site occupancy dynamics of 49 avian and one mammal species in forests dominated by ponderosa pine (*Pinus ponderosa*) on the Helena National Forest, Montana. Point count data were collected during the avian breeding seasons (May-July) of 2003-06 (pre-epidemic) and again during 2009-10 (during epidemic). We used a Bayesian hierarchical model that accounts for detection probability to obtain occupancy estimates for rare species as well as common ones. We used one model to investigate changes occupancy for all species with respect to the timing of the beetle outbreak and then used a second model to determine whether the relationships seen were associated to changes in snag density. Results show that 30% of species exhibited strong short-term associations between occupancy probability and the occurrence of the beetle epidemic and 12% of species exhibited strong short-term associations between occupancy probability and snag density. Predictions were partially met, as we saw short-term increases in occupancy probability for beetle-foraging species, decreases for some foliage-gleaning canopy insectivores, and intermediate amounts of change for many ground and shrub insectivores. While short-term ecological changes caused by a mountain pine beetle outbreak were associated with changes in occupancy rates for individual species, the overall species richness of native avifauna was unaffected. Though further study over a longer period of time will be necessary to understand the complete dynamics of this disturbance, our results suggest that well-planned salvage operations after beetle outbreaks could also maintain suitable habitat for successfully breeding avian species.

AVIAN COMMUNITY RESPONSE TO A MOUNTAIN PINE BEETLE EPIDEMIC

Introduction

Disturbances in western North American forests such as wildfire, prescribed fire, and timber management are well-studied, as are their impacts on wildlife (Hobbs and Spowart 1984, Russell et al. 2009, Saab et al 2007). Comparatively little is known about wildlife responses to large-scale insect epidemics (Martin et al. 2006) though the environmental importance of these disturbances is undisputed. Although the mountain pine beetle (*Dendroctonus ponderosae*) is a native part of the natural disturbance cycle of forests in western North America (Sartwell and Stevens 1975), fire suppression, climate, and logging have altered the typical interactions between insects and forests resulting in larger outbreaks of epidemic proportions (Carroll 2004, Parker et al. 2006, Bentz et al. 2010). A recent mountain pine beetle epidemic is the largest yet recorded in North America, affecting over 50 million acres of forest in British Columbia and the western United States (USDA Forest Service Rocky Mountain Region, British Columbia Ministry of Forests Lands and Natural Resource Operations 2011). This large-scale epidemic of mountain pine beetles will fundamentally alter the intermountain West, impacting management decisions related to fire and logging as well as wildlife management (Kaufmann et al. 2008).

Mountain pine beetle epidemics might benefit some avian wildlife, such as cavity-nesting woodpeckers. Hairy (*Picoides villosus*) and American three-toed woodpeckers (*P. tridactylus*) that consume mountain pine beetle larvae might be able to occur at

higher abundances and densities during and just after an epidemic (Drever and Martin 2010), although increases in fecundity have not been detected (Edworthy et al. 2010). Other species such as the mountain chickadee (*Poecile gambeli*) rely on conifer foliage for nesting and foraging, and might be adversely affected by mountain pine beetle epidemics (Bull 1983). Little is known about the full range of responses exhibited by the avian community after a beetle epidemic, or how those responses might change over time. This study investigates changes in occupancy probability during a beetle epidemic by a community of small landbirds detected during morning chorus point counts in a ponderosa pine (*Pinus ponderosa*) dominated forest in southwest Montana.

This study aims to estimate short-term avian changes in occupancy probability during a mountain pine beetle epidemic by using a hierarchical multi-species occupancy model (Dorazio et al. 2006, Russell et. al 2009, Ruiz-Gutierrez et al. 2010). Community-wide studies maximize the information available to managers and also provide an alternative to traditional management indicator species (MIS) approaches. While MIS studies are often less costly and logistically easier to implement, they also downplay the importance and variety of responses that management activities or disturbance might have on wildlife (Simberloff 1998, Niemi et al. 1997).

Hierarchical occupancy models account for variable and imperfect species' detections. The models also allow us to obtain unbiased estimates of species richness and community composition without masking or exacerbating direct and indirect effects (Zipkin et al. 2010). This information can be used by land managers trying to make decisions about post-beetle landscapes and can also be informative in the face of future

mountain pine beetle epidemics. We investigate species occupancy rates for 49 avian and one mammal species detected before and during the course of a mountain pine beetle epidemic. Our questions of interest are: 1) How are species occupancy rates influenced by the occurrence of a mountain pine beetle epidemic? 2) Are the changes in occupancy rates we observed attributed to tree mortality associated with the beetle epidemic? 3) How are local and global species richness influenced by the mountain pine beetle epidemic?

Avian Response Predictions

Beetle epidemics produce a pulse of food for some birds in the form of beetle larvae (Koplin 1969, Imbeau and Desrochers 2002, Drever et al. 2009). The increased availability of both nest (i.e., snags) and food (i.e., beetle larvae) substrates might result in positive changes in occupancy for cavity-nesting, beetle-foraging species, such as the American three-toed woodpecker.

Other bird groups might be adversely affected by a mountain pine beetle epidemic. Species that use conifer foliage for nest placement or foraging substrate, such as the yellow-rumped warbler (*Setophaga coronata*) or mountain chickadee (Behle 1956, Reilly 1968) were expected to decline following conifer foliage desiccation and subsequent losses in nesting habitat and foliage invertebrates.

Minimal changes in ground and shrub vegetation are expected during beetle epidemics (Jenkins et al. 2008). Immediately following in the post-epidemic stage, however, there might be large increases in understory shrub and herbaceous vegetation (Stone and Wolfe 1996, Page and Jenkins 2007, Jenkins et al. 2008). Since our study was

conducted prior to and early during the epidemic, we did not expect changes in occupancy rates by ground- and shrub-foraging species such as hermit thrush (*Catharus guttatus*) and MacGillivray's warbler (*Geothlypis tolmiei*) (Jones and Donovan 1996, Pitocchelli 1995). Omnivorous birds that specialize on pine seeds, however, such as Clark's nutcracker (*Nucifraga columbiana*) (Tomback 1978) were expected to experience decreases in occupancy probability following diminishing sources of pine cones.

Most woodpecker species prefer snags to live trees for foraging, drumming, and nesting (Scott 1979, Imbeau and Desroches 2002), and we expected increased occupancy for these species as the beetle epidemic progressed. Therefore, we anticipated that the number of sites (survey stations) occupied by these species would likely increase during the beetle epidemic and translate into a small increase in average local species richness (the average number of species occupying one site). Rapid reactions to habitat changes after a disturbance, such as a beetle outbreak, are not expected for most other species because of time lags created by site tenacity of breeding birds (Wiens and Rotenberry 1985). In a 10-year study of a forest bird community in British Columbia, habitat changes following a mountain pine beetle epidemic were found to only weakly regulate species richness (Drever et al. 2009). Therefore, while we acknowledged that the percent area occupied by various species might change, we did not expect to see changes in global species richness (total number of species within the entire study area).

Methods

Study Area

Four study units ranging from 130 to 260 hectares were selected based on management priorities within the northern Elkhorn Mountains of the Helena National Forest in Montana, USA (Figure 1). The 300,000 acre Elkhorn Wildlife Management Area (WMA) is an island mountain range in southwest Montana, cooperatively managed by several federal, state, and private entities. The original study was part of an Interior West-wide Birds and Burns Network project designed to evaluate the effectiveness of prescribed fire treatments in fuels reduction and subsequent effects on habitats and populations of the associated avifauna (Saab et al. 2006, Fowler et al. 2008, Russell et al. 2009). Pre-treatment data from point count surveys were collected in each study unit during four bird breeding seasons (2003-2006) and pre-treatment vegetation data were collected in 2003, but in 2006 litigation prevented the implementation of the prescribed fire treatments. Mountain pine beetle attacks began in the Helena National Forest in 2006, peaked in 2008, and continued through 2009-2010 when beetle-caused tree mortality was reduced (Bentz et al. unpublished data). Point count surveys were conducted again near the end of the epidemic in the summers of 2009-2010, along with vegetation surveys in 2010.

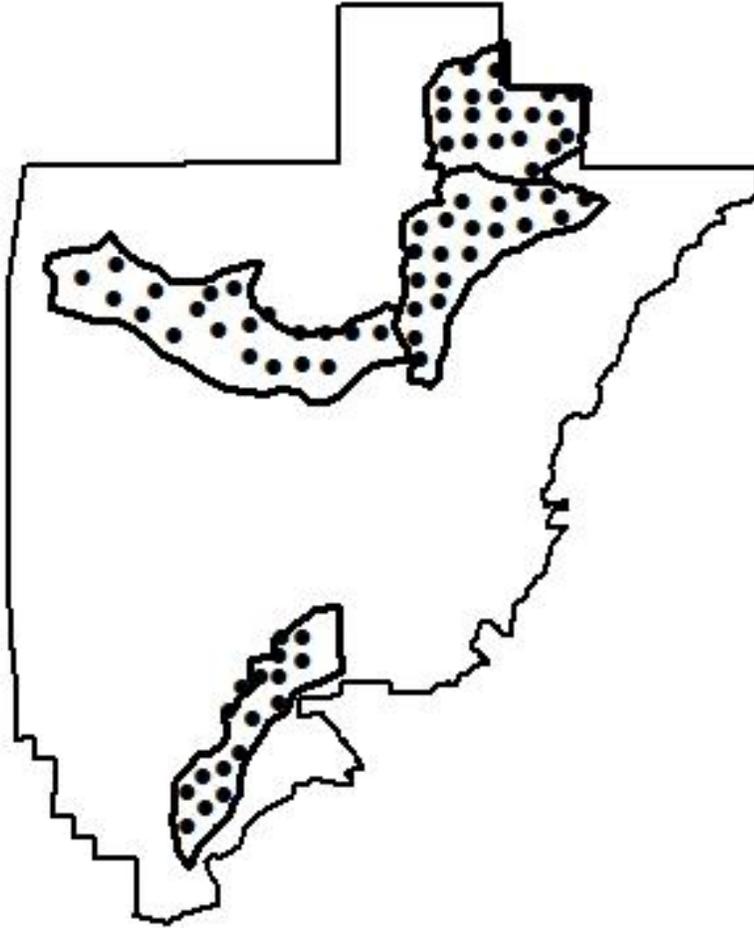


Figure 1. Map of four study units containing 76 point count stations in the Elkhorn Wildlife Management Unit in the Helena National Forest (Montana, USA).

The study units are characteristic of dry mixed coniferous forests, largely dominated by ponderosa pine with lesser amounts of Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*). The study units also contain stands of quaking aspen (*Populus tremuloides*), found mainly along snow melt drainages and creeks. The understory vegetation is dominated by snowberry (*Symphoricarpos albus*), Oregon grape (*Berberis repens*), and kinnickinnick (*Arctostaphylos uva-ursi*). Ground cover is sparse under dense conifer forest, though a sparse grass covering comprised of bluebunch

wheatgrass (*Pseudoroegneria spicatus*) and Idaho fescue (*Festuca idahoensis*) occurs where canopy cover allows more light to reach ground level.

Survey Methods

Point Counts: In 2002, we established approximately 20 point count stations in each of 4 study units, resulting in a total of 76 point count stations (Figure 1). Stations were randomly placed but were located ≥ 250 m apart and ≥ 150 m from a study unit boundary. We attempted to visit each station bi-weekly from 22 May and 3 July during the years 2003-2006 (pre-epidemic) and 2009-10 (during-epidemic) for a total of 3 visits per station per season. To ensure a standard level of bird activity, point counts were conducted just after the dawn chorus in fair weather only. The point count sampling began just after sunrise and was completed within five hours. At each point, a single observer recorded all birds detected during a 5-minute count period, and estimated the distance to each observed individual in distance classes. The data used in our analyses were truncated at 75m because accurately estimating distances beyond 67m is difficult (Alldredge et al. 2007) for most observers.

Forty-eight avian species, one avian group, and one mammal (American red tree squirrel [*Tamiasciurus hudsonicus*]) were detected at distances of 75 m or less over the course of the study. The American red tree squirrel is a nest predator of many small landbirds, especially in conifer-dominated forests with minimal fragmentation (Sieving and Willson 1998, Tewksberry et al. 1998). The fact that these vocal mammals are often

detected in point-count surveys gave us the unique opportunity to monitor occupancy and detection trends of this non-avian member of the forest community.

Habitat Measurements: To quantify the habitat changes associated with the mountain pine beetle epidemic, we measured snag density at each of our 76 point count stations once before the beetle epidemic (in 2002-03) and again during the end of the epidemic (2010). At each station, the vegetation plot was 2.5 ha in size and consisted of intersecting 20m x 100m rectangles in a cross plot design (Saab et al. 2006; Figure 2). These vegetation plots were centered on the same focal tree that the point count surveys were centered on. Wildlife snags were defined as any standing dead (at least 50% of the needles dead or missing) tree ≥ 1.4 m in height and larger than 23 cm in diameter at breast height (DBH). At each vegetation plot, all wildlife snags within 10m to either side of a 50m transect were tallied. This survey was repeated in each cardinal direction. The total number of snags counted per plot was then divided by the total area surveyed ($20 \times 50 \times 4 = 4000\text{m}^2$ per plot) to create the snag density covariate.

Modeling Philosophy

Our first question of interest was: How do species occupancy probabilities change during a mountain pine beetle epidemic? We evaluated this question using a single primary model. Using secondary models that included a snag density covariate, we subsequently evaluated the degree to which beetle-induced changes in snag densities were associated with changes observed in the primary model. Since these simple questions could be addressed by single models, we felt that model selection was

unnecessary. By employing a Bayesian framework, our inferences were evaluated with equal-tail credible intervals (CRIs) about the importance of estimated parameters. For ease of interpretation, we chose to provide the most in-depth discussion for species with 95% CRIs that do not contain 0, though we present probability statements for all species and recognize that these might also indicate meaningful relationships with probabilities close to those that we describe in detail.

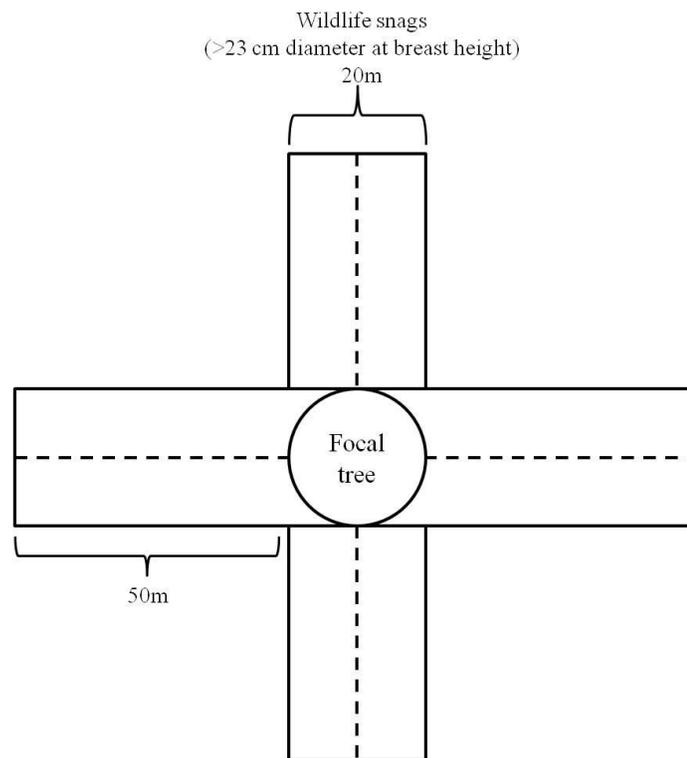


Figure 2. Schematic of vegetation plot. All snags > 23 cm dbh within 10m to either side of 4 50-m belt transects were counted.

Model

Observations were made in 6 primary sampling occasions (e.g., years).

Occupancy probability for a species of interest on a given site might change across

primary occasions due to colonization and extinction of sites. Within each primary sampling period, 3 secondary sampling occasions (e.g., visits) occur over a time where the population of interest is assumed to be closed to demographic changes (the avian breeding season). This type of sampling design is typically referred to as the “robust design” (Pollock 1982). The information collected during secondary sampling occasions is used to account for imperfect detection (MacKenzie 2006). Although species-specific detection probabilities might vary with respect to variation over spatial extent, primary sampling period, or secondary sampling period, variation in detection probability might also reflect variation in species abundances over these same scales (Royle and Nichols 2003). We used a Bayesian hierarchical multispecies occupancy model (Russell et al. 2009, Dorazio and Royle 2005, Dorazio et al. 2006) to model site occupancy and detection probabilities for all species detected before and/or during the beetle epidemic and also to link all species at the community-level. Sharing information among species from the same community (‘borrowing strength from the ensemble’ Morris 1983) uses available data more efficiently, resulting in more precise species-specific estimates of occupancy and detection probabilities (Kéry et al. 2009; Zipkin et al. 2009).

Primary Models: In these models, the state process (within year site occupancy) was treated as a latent variable (z) such that $z = 1$ if the site is truly occupied by the species of interest in a particular year and $z = 0$ if the site is unoccupied. The latent process z_{ijt} is a Bernoulli random variable such that a site j will be occupied by species i in year t with probability ψ_{ib} , where b represents the two outbreak periods modeled: before and during the beetle event.

Logit(ψ_{ib}) was linearly related to a species-specific intercept and a species-specific difference in occupancy between pre- and during-epidemic conditions ($\text{beet}_b = 0$ before the epidemic and 1 during). In our model, we assumed that species-specific occupancy across sites was constant within outbreak period. Though the latent variable (z_{ijt}) might have changed every year, the occupancy probability for a species was assumed to be constant across all sites within each outbreak period (if $t = 1:4$, $b = \text{before}$; if $t = 5:6$, $b = \text{during}$). Thus,

$$z(i,j,t) \sim \text{Bernoulli}(\psi_{ib}) \text{ and}$$

$$\text{logit}(\psi_{ib}) = \beta_{0i} + \beta_{1i} * \text{beet}_b.$$

The observation process x was treated as a Bernoulli random variable such that species i was observed at a site j , during visit k , in period b , with probability of detection p_{ijkb} given that the species was truly present ($z_{ijt} = 1$). Logit(p_{ijkb}) was linearly related to a species-specific intercept and the species-specific difference in detection probability between pre- and during-epidemic conditions. Because we did not incorporate site- or visit-level covariates, we assumed that p_{ijkb} varied only by species and outbreak period. Thus,

$$x(i,j,k,t) \sim \text{Bernoulli}(p(i,b)*z(i,j,t)) \text{ and}$$

$$\text{logit}(p_{ib}) = \alpha_{0i} + \alpha_{1i} * \text{beet}.\text{ind}_b.$$

Colonization and extinction rates are modeled implicitly in the above models with yearly site colonization and extinction rates constrained to being equal to one another.

These models allow colonization and extinction rates to take on three different values:

one value before epidemic, one value at the transition between pre- and during-beetle years, and one value during epidemic. The probability that a site unoccupied at time t will become occupied at time $t+1$ is the probability of colonization. Extinction probability is the probability that a site that was occupied at time t will be unoccupied at time $t+1$.

Secondary Models: The above models were used to explore the relationships between various species or guilds of interest and the occurrence of the beetle epidemic. We also applied a secondary model containing a snag density covariate for occupancy probability to investigate whether the species-specific changes discovered in the first model were adequately explained by site- and period-level changes in snag density (snag_{jb}). Here, species- and site- and period- specific occupancy probability was a function of a species-specific intercept and the species-specific relationship with snag density. Detection probability was modeled as before:

$$\text{logit}(\psi_{ijb}) = \beta_{0i} + \beta_{1i} * \text{snag}_{jb}$$

$$\text{logit}(p_{ib}) = \alpha_{0i} + \alpha_{1i} * \text{beet}_b.$$

These models assumed that differences in snag density are the only source of explained site-to-site heterogeneity in occupancy probabilities, and that no temporal variation in occupancy rates is present aside from that which can be attributed to changes in snag density. Again, these models allow for yearly colonization and extinction events though the rates are constrained to being equivalent within a time period.

Species Richness: Both local (site-level) and global (study area-level) species richness before and during the beetle epidemic were calculated and compared using latent variable (z) estimates from the primary model. Average local species richness (\bar{L}) in a year (t) is the estimated average species richness across sites within that year, where $nsites$ is the total number of sites and $nspec$ is the total number of species.

$$\bar{L}(t) = \frac{1}{nsites} \sum_{i=1}^{nspec} \sum_{j=1}^{nsites} z(i, j, t)$$

Global species richness (G) was computed as the total number of species occupying the entire study area in a given year.

$$G(t) = \sum_{i=1}^{nspec} \begin{cases} 1 & \text{if } \sum_{j=1}^{nsites} z(i, j, t) \geq 1 \\ 0 & \text{if } \sum_{j=1}^{nsites} z(i, j, t) < 1 \end{cases}$$

Program: The data were analyzed using WinBUGS (Spiegelhalter et al. 2003), a tool for Bayesian inference (Appendix C). WinBUGS was called from the open-source statistical computing environment R (version 2.13.1; R Development Core Team 2011) using the R2WinBUGS (Sturtz et al. 2005) package. The results were exported and manipulated as R objects. Convergence was assessed using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). A goodness-of-fit test was not performed for this analysis due to the simplicity of the models used.

Results

Forty-eight avian species, one avian group (unidentified *Empidonax* flycatcher) and one mammal (American red tree squirrel) were detected at distances of ≤ 75 m over the course of the study (Appendix A).

The most commonly detected species were red-breasted nuthatch (*Sitta canadensis*), American red tree squirrel, yellow-rumped warbler, dark-eyed junco (*Junco hyemalis*), and mountain chickadee (Appendix A). These detections occurred over the course of 6 seasons during both pre-epidemic (2003-06) and epidemic (2009-10) conditions.

Primary Model (Covariate Effects and Guild-level Responses)

We found convincing evidence (95% credible interval did not contain zero) of associations between occupancy probability and the beetle epidemic for 15 species, suggestive evidence (90% credible interval did not contain 0) for 18 species, and moderate evidence (85% credible interval did not contain 0) for 21 species (Table 1). In each of these cases, just one of the associations was negative (black-capped chickadee [*Poecile atricapillus*], Figure 3). Occupancy probability estimates for the species exhibiting the strongest evidence of change are shown in Figure 4.

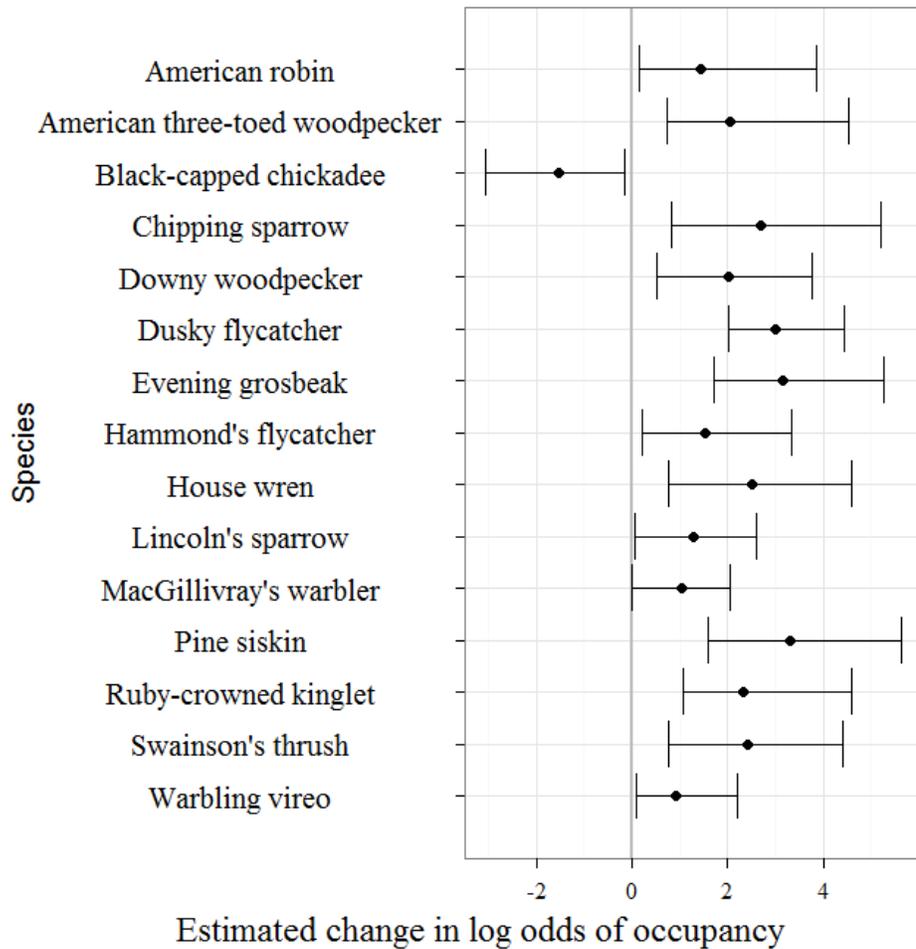


Figure 3. Estimates of β_1 (change in log odds occupancy associated with the beetle epidemic) for 15 species showing strong evidence of changes (i.e., 95% credible intervals do not contain zero).

Table 1. $\Pr(\beta_1 < 0)$, $\Pr(\beta_1 > 0)$, and foraging guild for all species from the primary model posterior distributions. Guilds were assigned according to Airola and Barrett (1985), Pitocchelli (1995), Jones and Donovan (1996), Hunt and Flaspohler (1998), McCallum et al. (1999), Gardali and Ballard (2000), Saab and Powell (2005), Swanson et al. (2008), Foote et al. (2010), and Gilbert et al. (2010) here and in other tables throughout this thesis.

Species	Foraging Guild	$\Pr(\beta_1 < 0)$	$\Pr(\beta_1 > 0)$
American red tree squirrel			0.81
American robin***	GI		0.99
American three-toed woodpecker***	BI		1
Barred owl	CA	0.66	
Black-capped chickadee***	CI	0.98	
Black-headed grosbeak	OM		0.86
Brown creeper	BI		0.5
Brown-headed cowbird*	OM		0.95
Cassin's finch**	OM		0.96
Cassin's vireo	SI		0.57
Chipping sparrow***	OM		1
Clark's nutcracker	OM	0.73	
Common raven**	OM		0.97
Dark eyed-junco	OM		0.79
Downy woodpecker***	BI		1
Dusky flycatcher***	AI		1
Dusky grouse	OM	0.68	
Evening grosbeak***	OM		1
Gray jay	OM		0.65
Hairy woodpecker*	BI		0.93
Hammond's flycatcher***	AI		0.99
Hermit thrush	GI		0.64
House wren***	GI		1
Lazuli bunting	OM	0.88	
Lincoln's sparrow***	OM		0.98
MacGillivray's warbler***	SI		0.98
Mountain bluebird**	AI		0.96
Mountain chickadee	CI	0.75	
Mourning dove	OM	0.82	
Northern flicker*	OM		0.93
Northern goshawk	CA		0.82
Orange-crowned warbler	SI	0.53	
Pileated woodpecker	OM	0.64	
Pine siskin***	OM		1
Red crossbill	OM	0.88	
Red-breasted nuthatch	BI	0.56	
Red-naped sapsucker	OM		0.81
Red-tailed hawk	CA		0.86
Ruby-crowned kinglet***	CI		1
Ruffed grouse	OM		0.84
Steller's jay	OM		0.84
Swainson's thrush***	SI		1

Table 1 Continued

Townsend's solitaire	AI	0.58	
Tree swallow	AI		0.85
Unidentified Empidonax flycatcher	AI	0.91	
Vesper sparrow	OM	0.53	
Warbling vireo***	CI		0.99
Western tanager	OM		0.91
White-breasted nuthatch	BI	0.74	
Yellow-rumped warbler	CI		0.72

*** 95% CRI does not contain 0

**90% CRI does not contain 0

*85% CRI does not contain 0

Columns represent foraging guild (AI = aerial insectivore, BI = bark insectivore, CI = canopy foliage insectivore, GI = ground insectivore, OM = omnivore, and SI = shrub foliage insectivore). The species are listed in phylogenetic order.

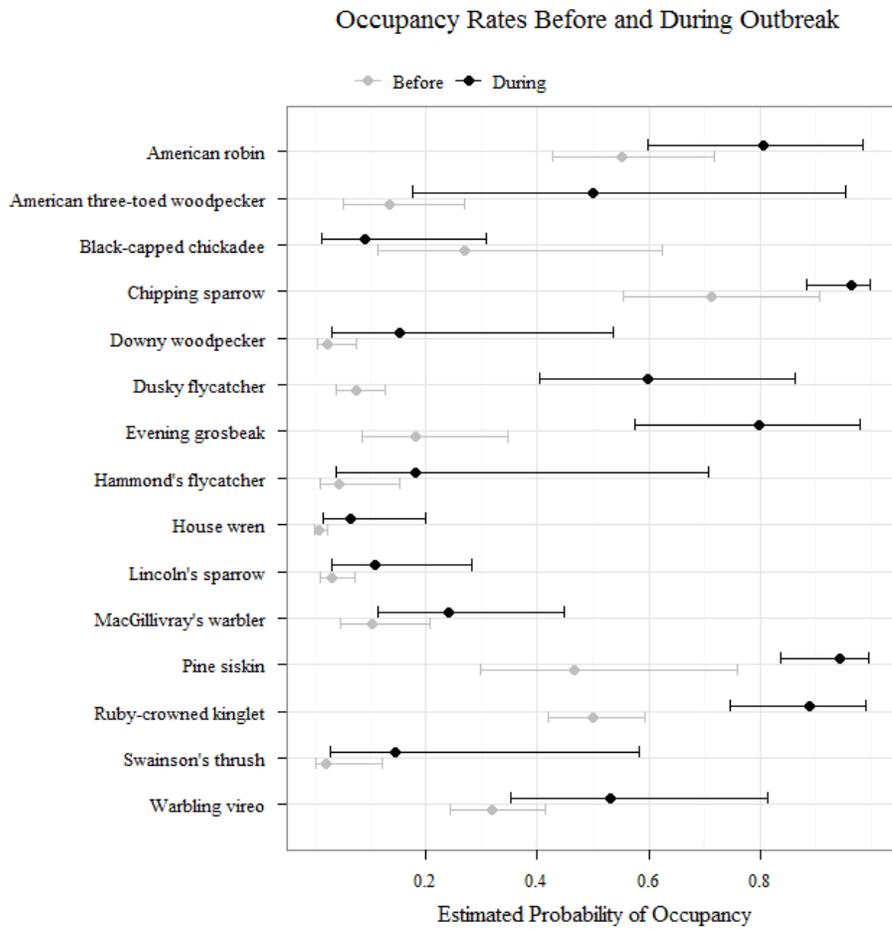


Figure 4. Estimates of occupancy probabilities and 95% credible intervals before and during beetle epidemic for the 15 species showing strong evidence of changes.

The prediction that bark-insectivore occupancy probabilities would be positively associated with the beetle epidemic was partially met. We found evidence of positive changes for three cavity-nesting bark insectivores (American three-toed, downy [*Picoides pubescens*] and hairy woodpecker) (Table 1 and Figure 5). We did not detect evidence of positive changes for other insectivores such as brown creeper (*Certhia americana*), red-breasted nuthatch, and white-breasted nuthatch (*Sitta carolinensis*).

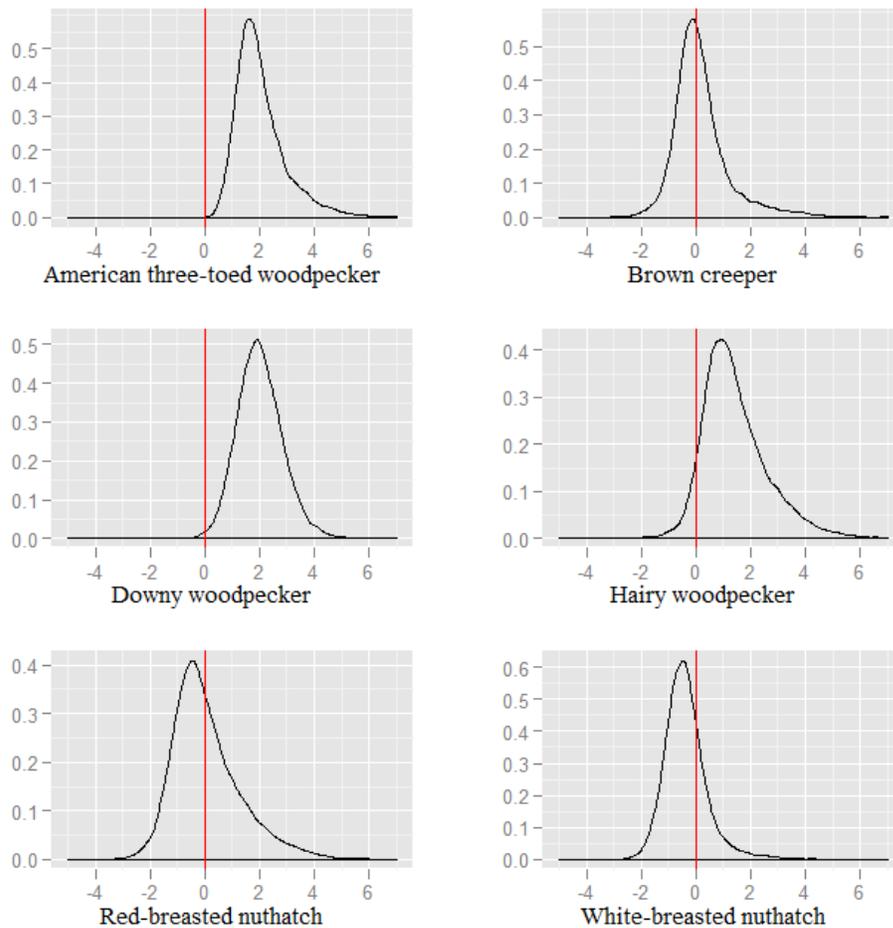


Figure 5. Posterior probability distributions for β_1 from the primary model for all bark insectivores included in the analysis.

Our prediction that canopy-level foliage insectivores would experience occupancy declines was largely not met. We found evidence of negative changes in occupancy for black-capped chickadee and mountain chickadee, evidence of positive changes in occupancy for ruby-crowned kinglet (*Regulus calendula*), and warbling vireo (*Vireo gilvus*), and no evidence of change for Cassin's vireo (*Vireo cassinii*) and yellow-rumped warbler (Table 1 and Figure 6).

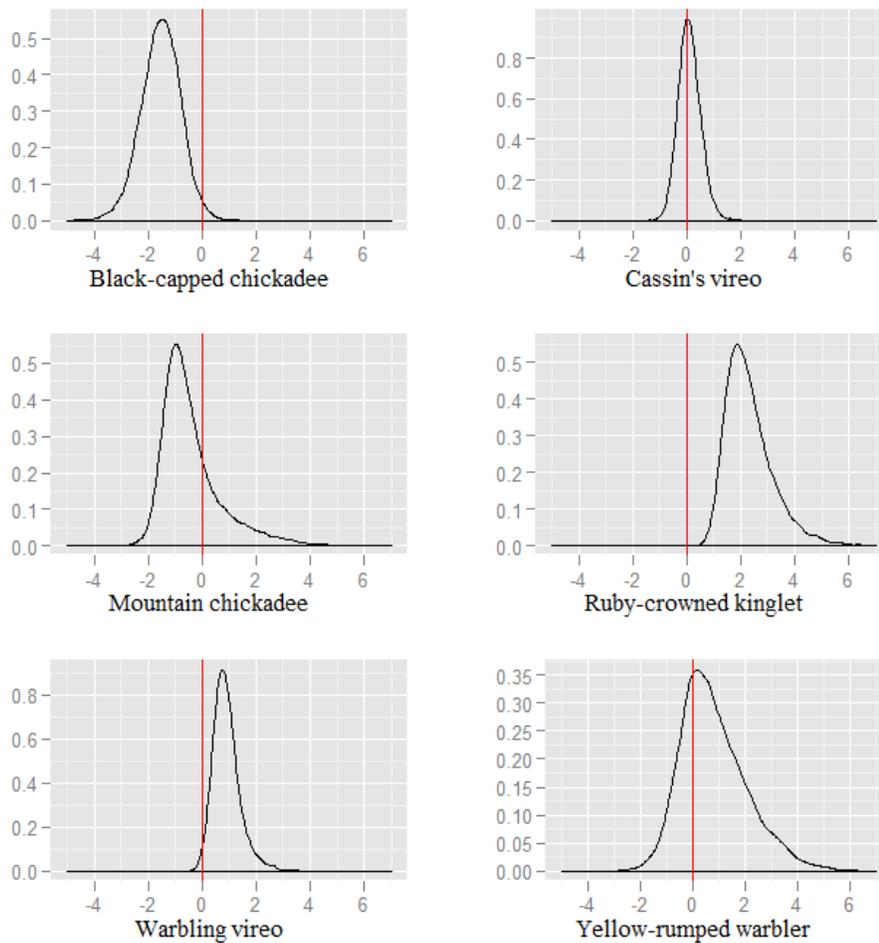


Figure 6. Posterior probability distributions for β_1 from the primary model for all canopy-level foliage insectivores included in the analysis.

We predicted that ground and shrub insectivores would experience no changes in occupancy at this stage of the epidemic, and that prediction was partially met. While we found little evidence of change for hermit thrush and orange-crowned warbler (*Oreothlypis celata*), we did find some evidence of positive associations between occupancy probabilities and the beetle epidemic for other ground and shrub insectivores including American robin (*Turdus migratorius*), house wren (*Troglodytes aedon*), MacGillivray's warbler (*Geothlypis tolmie*), and Swainson's thrush (*Catharus ustulatus*) (Table 1 and Figure 7).

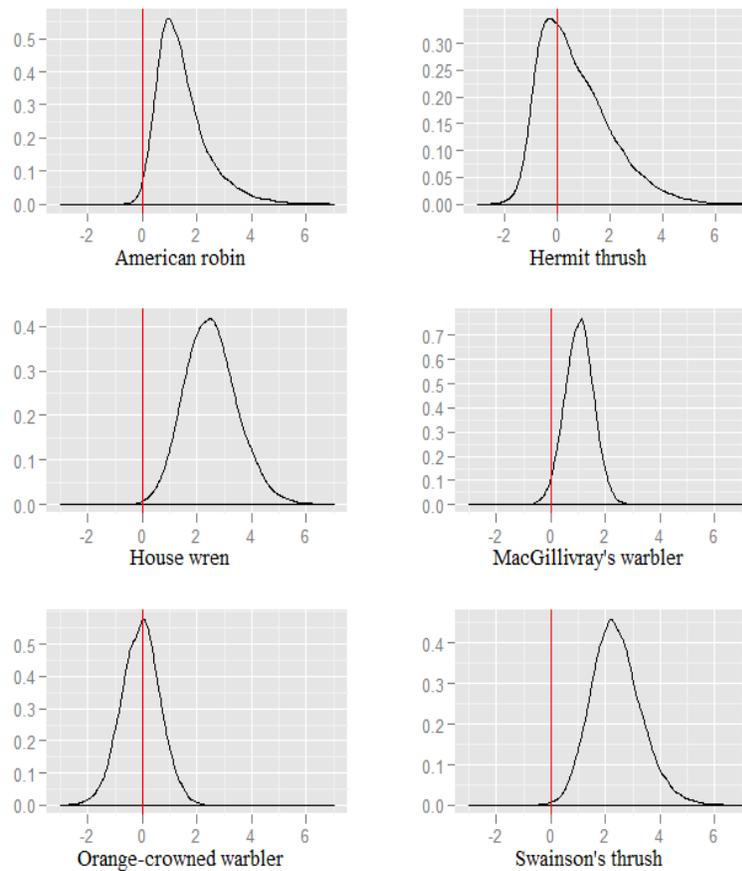


Figure 7. Posterior probability distributions for β_1 from the primary model for all ground and shrub insectivores included in the analysis.

In accordance with our prediction, we saw some evidence of negative associations between occupancy probabilities and the beetle epidemic for the two seed specialists in the analysis, Clark's nutcracker and red crossbill (*Loxia curvirostra*) (Table 1 and Figure 8).

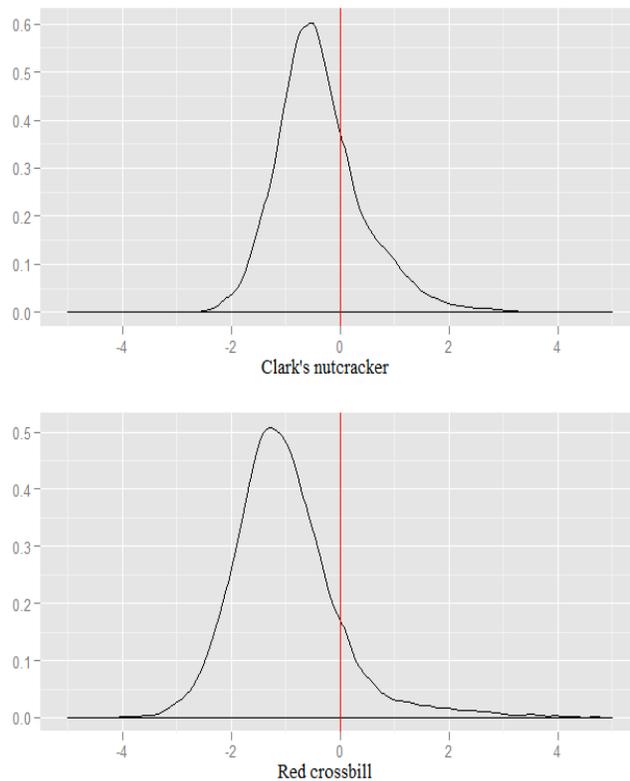


Figure 8. Posterior probability distributions for β_1 from the primary model for all seed specialists included in the analysis.

We also saw strong positive relationships between occupancy probabilities and the beetle epidemic for 2 aerial insectivores (dusky and Hammond's flycatchers [*Empidonax oberholseri* and *E. hammondi*]) and 4 omnivores (chipping sparrow [*Spizella passerina*], evening grosbeak [*Coccothraustes vespertinus*], Lincoln's sparrow [*Melospiza lincolnii*], and Pine siskin [*Spinus pinus*]).

We did not anticipate changes in detection probability, but found evidence of a strong negative association (95% CRI does not overlap 0) between detection probability and the beetle epidemic for 6 species, suggestive evidence (90% credible interval did not contain 0) for 10 species and moderate evidence (85% credible interval did not contain 0) for 14 species (Table 2). These species represent a variety of foraging groups.

Table 2. $\Pr(\alpha_1 < 0)$, $\Pr(\alpha_1 > 0)$, and foraging guild for all species from the primary model posterior distributions.

Species	Foraging Guild	$\Pr(\alpha_1 < 0)$	$\Pr(\alpha_1 > 0)$
American red tree squirrel***		1.00	
American robin	GI	0.56	
American three-toed woodpecker	BI	0.90	
Barred owl	CA	0.73	
Black-capped chickadee	CI	0.88	
Black-headed grosbeak	OM	0.90	
Brown creeper	BI	0.82	
Brown-headed cowbird	OM		0.65
Cassin's finch	OM	0.91	
Cassin's vireo**	SI	0.97	
Chipping sparrow	OM		0.91
Clark's nutcracker*	OM	0.94	
Common raven***	OM	0.98	
Dark eyed-junco***	OM	1.00	
Downy woodpecker*	BI	0.94	
Dusky flycatcher	AI	0.81	
Dusky grouse	OM	0.60	
Evening grosbeak	OM		0.67
Gray jay**	OM	0.96	
Hairy woodpecker	BI	0.67	
Hammond's flycatcher**	AI	0.96	
Hermit thrush***	GI	1.00	
House wren	GI	0.78	
Lazuli bunting	OM	0.77	
Lincoln's sparrow	OM	0.82	
MacGillivray's warbler	SI		0.51
Mountain bluebird	AI	0.67	
Mountain chickadee***	CI	1.00	
Mourning dove*	OM	0.95	
Northern flicker	OM	0.84	
Northern goshawk	CA	0.65	
Orange-crowned warbler	SI	0.77	
Pileated woodpecker	OM	0.91	

Table 2 Continued

Pine siskin	OM		0.88
Red crossbill**	OM	0.96	
Red-breasted nuthatch	BI	0.91	
Red-naped sapsucker	OM	0.89	
Red-tailed hawk	CA	0.86	
Ruby-crowned kinglet	CI	0.92	
Ruffed grouse	OM	0.80	
Steller's jay	OM	0.57	
Swainson's thrush	SI	0.89	
Townsend's solitaire***	AI	0.99	
Tree swallow	AI	0.87	
Unidentified Empidonax flycatcher	AI	0.60	
Vesper sparrow	OM	0.84	
Warbling vireo	CI	0.89	
Western tanager	OM	0.73	
White-breasted nuthatch	BI	0.83	
Yellow-rumped warbler*	CI	0.93	

*** 95% CRI does not contain 0

**90% CRI does not contain 0

*85% CRI does not contain 0

Secondary Model

We found convincing evidence (95% credible interval did not contain zero) of associations between occupancy probability and snag density for 4 species and suggestive evidence (90% credible interval did not contain 0) for 11 species (no moderate evidence [85% credible interval did not contain 0] was found) (Table 3 and Figure 9). The only negative association found was for the black-capped chickadee.

Table 3. $\Pr(\beta_1 < 0)$, $\Pr(\beta_1 > 0)$, and foraging guild for all species from the secondary model posterior distributions.

Species	Foraging Guild	$\Pr(\beta_1 < 0)$	$\Pr(\beta_1 > 0)$
American red tree squirrel			0.67
American robin	GI		0.62
American three-toed woodpecker***	BI		0.98
Barred owl	CA	0.59	
Black-capped chickadee**	CI	0.96	
Black-headed grosbeak	OM		0.52

Table 3 Continued

Brown creeper	BI		0.51
Brown-headed cowbird	OM	0.76	
Cassin's finch**	OM		0.96
Cassin's vireo	SI	0.91	
Chipping sparrow	OM		0.76
Clark's nutcracker	OM		0.51
Common raven**	OM		0.96
Dark eyed-junco	OM	0.55	
Downy woodpecker	BI		0.90
Dusky flycatcher***	AI		1.00
Dusky grouse	OM	0.69	
Evening grosbeak***	OM		1.00
Gray jay	OM		0.47
Hairy woodpecker**	BI		0.95
Hammond's flycatcher**	AI		0.96
Hermit thrush	GI		0.51
House wren	GI		0.76
Lazuli bunting	OM	0.83	
Lincoln's sparrow	OM		0.65
MacGillivray's warbler	SI		0.86
Mountain bluebird	AI		0.77
Mountain chickadee	CI	0.74	
Mourning dove	OM	0.81	
Northern flicker	OM		0.66
Northern goshawk	CA		0.92
Orange-crowned warbler	SI		0.63
Pileated woodpecker	OM	0.63	
Pine siskin**	OM		0.96
Red crossbill	OM	0.89	
Red-breasted nuthatch	BI	0.61	
Red-naped sapsucker	OM		0.59
Red-tailed hawk	CA	0.65	
Ruby-crowned kinglet***	CI		1.00
Ruffed grouse	OM	0.52	
Steller's jay	OM		0.79
Swainson's thrush**	SI		0.96
Townsend's solitaire	AI	0.59	
Tree swallow	AI	0.50	0.50
Unidentified Empidonax flycatcher	AI	0.84	
Vesper sparrow	OM	0.59	
Warbling vireo	CI	0.69	
Western tanager	OM		0.88
White-breasted nuthatch	BI	0.70	
Yellow-rumped warbler	CI		0.55

*** 95% CRI does not contain 0

**90% CRI does not contain 0

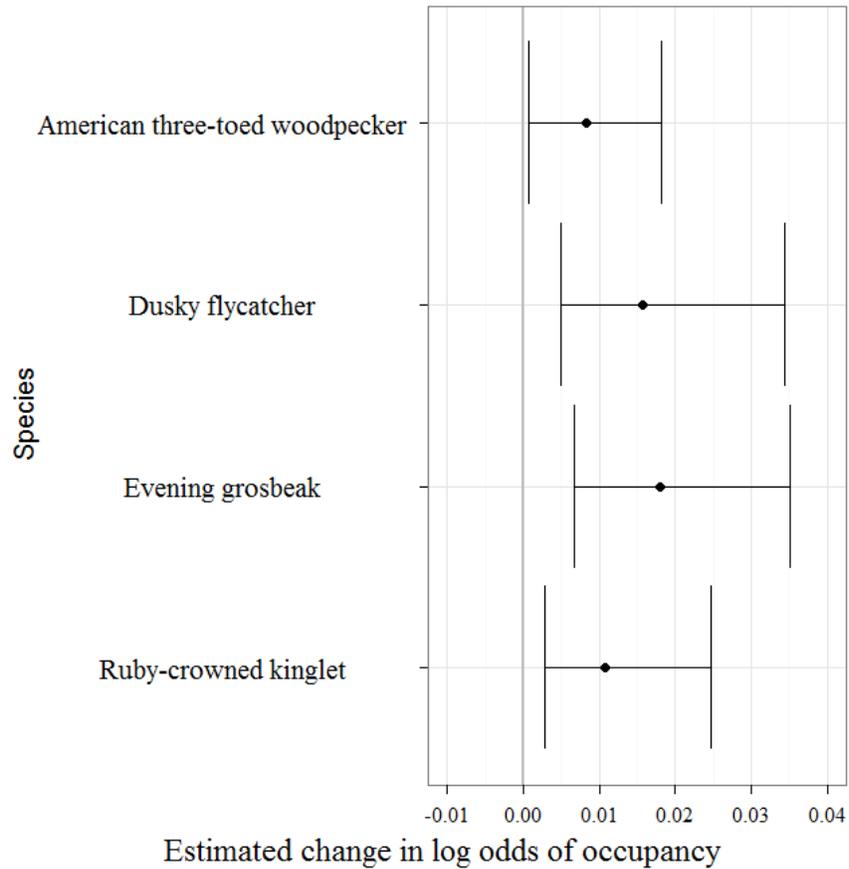


Figure 9. Estimates of β_1 (change in log odds occupancy associated with snag density) for 4 species showing strong evidence of changes (i.e., 95% credible intervals do not contain zero).

For bark insectivores, the results from the snag model generally agreed with the primary model (Table 3 and Figure 10). We found evidence for positive associations with snag density for American three-toed, downy, and hairy woodpeckers. The magnitude and direction of change was unclear for the three non-woodpecker bark insectivores.

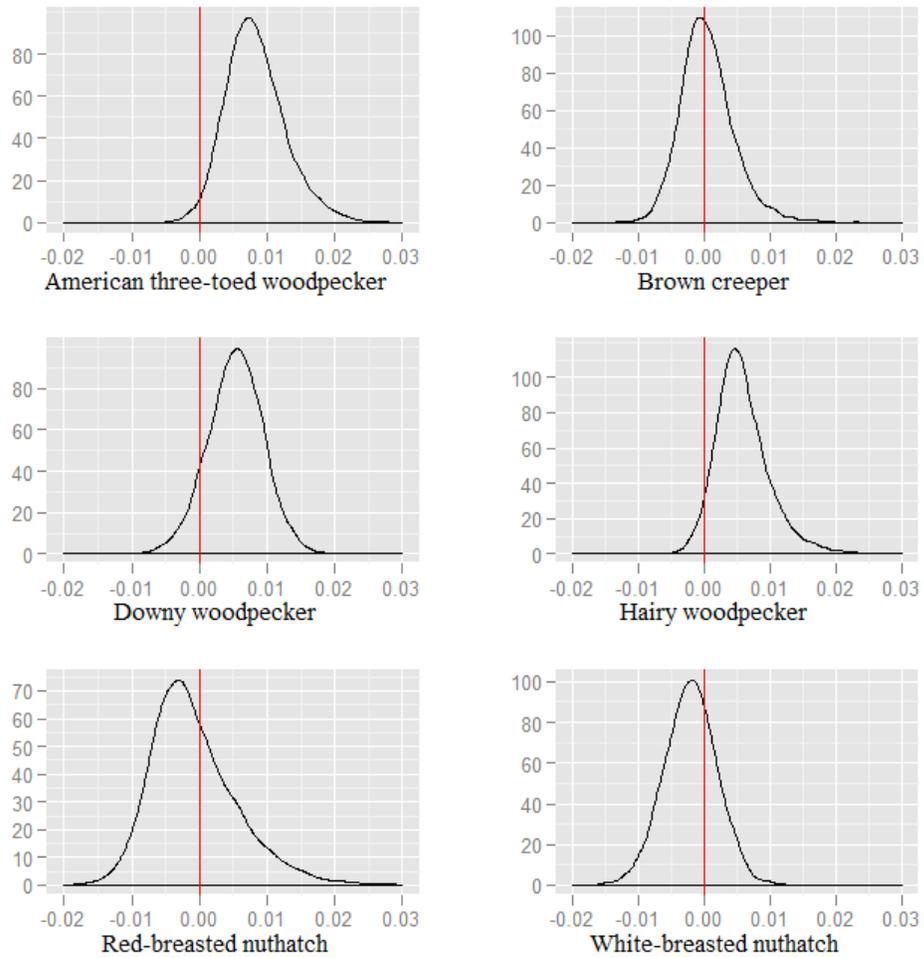


Figure 10. Posterior probability distributions for β_1 from the secondary model for all bark insectivores included in the analysis.

Our prediction that canopy-level foliage insectivores would be negatively associated with snag density was largely not met (Table 3 and Figure 11). We did find some evidence of negative relationships between occupancy probability and snag density for black-capped chickadee and Cassin's vireo, but found no evidence of association for mountain chickadee, warbling vireo, and yellow-rumped warbler. Contrary to our prediction, we found a strong positive relationship between occupancy probability and snag density for ruby-crowned kinglet.

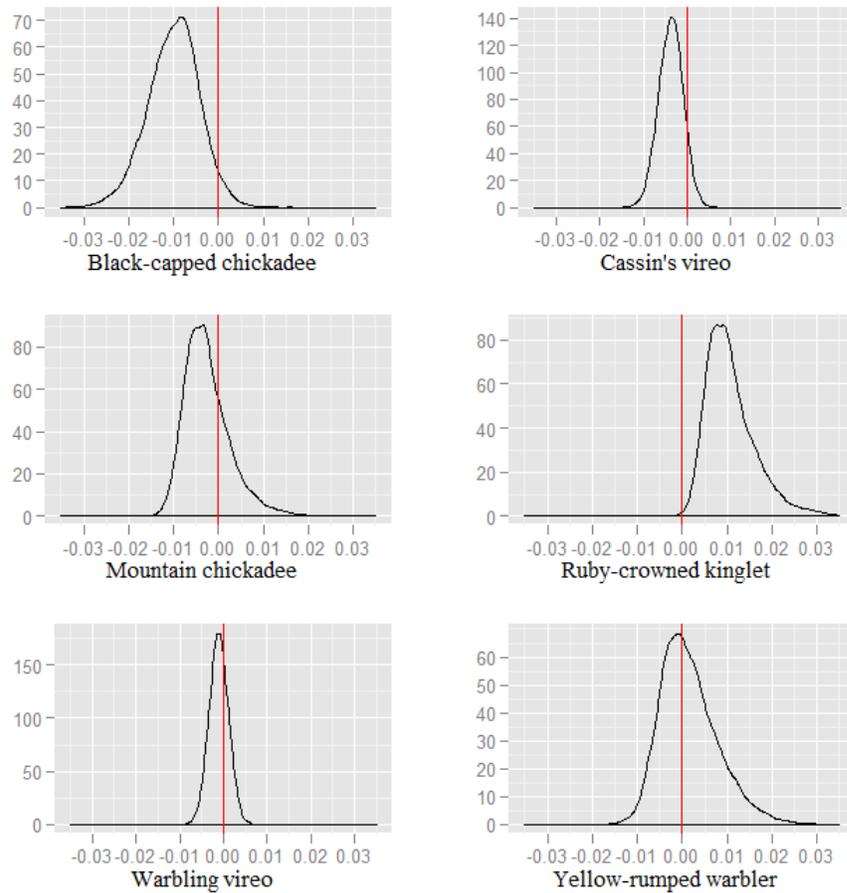


Figure 11. Posterior probability distributions for β_1 from the secondary model for all canopy-level foliage insectivores included in the analysis.

We predicted that the relationship between ground and shrub insectivore occupancy probabilities and snag density would be minimal, and that prediction was partially met (Table 3 and Figure 12). We saw no evidence of changes for 5 of the 6 species in our analysis, and strong evidence of positive change for 1 shrub insectivore (Swainson's thrush).

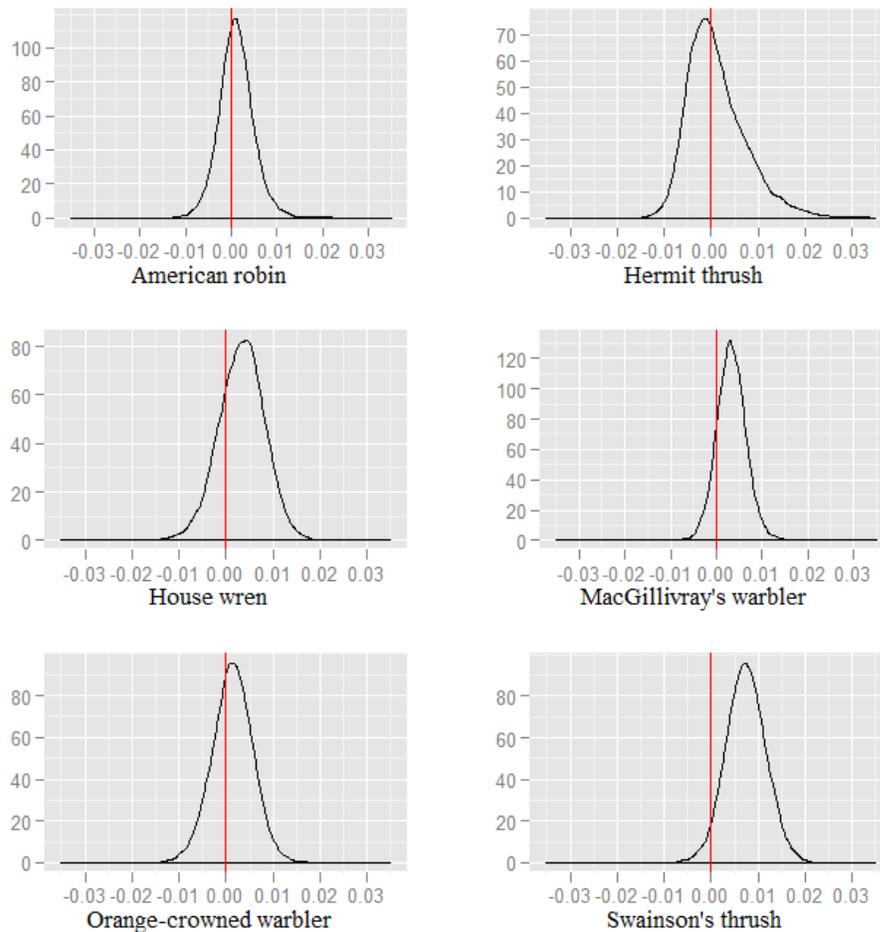


Figure 12. Posterior probability distributions for β_1 from the secondary model for all ground and sbrub insectivores included in the analysis.

In accordance with our prediction, we did see some evidence of a negative association between occupancy probability and snag density for the seed specialist red crossbill, though we found no evidence of change for Clark's nutcracker (Table 3 and Figure 13). Occupancy rates for the omnivorous evening grosbeak, the foliage-gleaning ruby-crowned kinglet, and the dusky flycatcher (an aerial insectivore) were also strongly

associated with snag density, though we did not find evidence of similar relationships for other members of these guilds (Table 3).

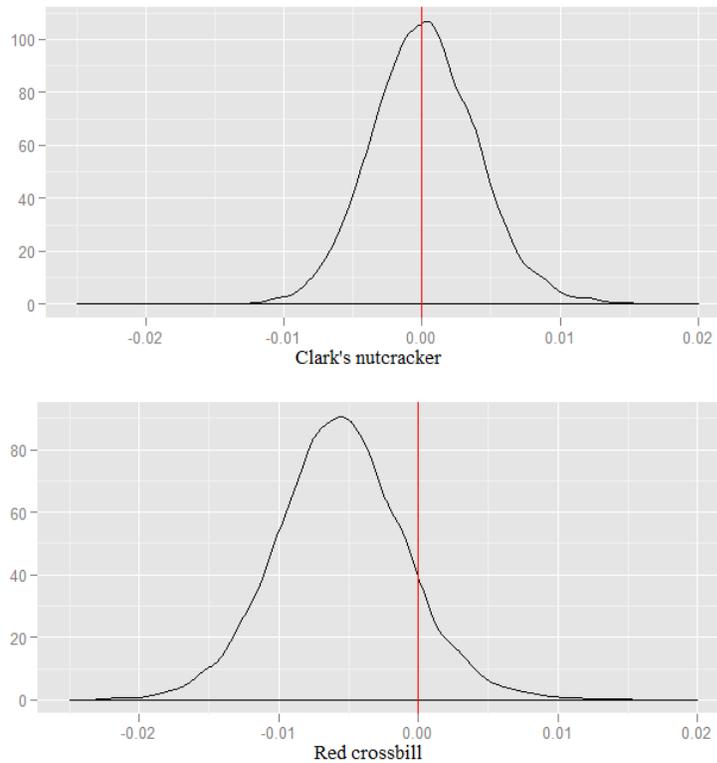


Figure 13. Posterior probability distributions for β_1 from the secondary model for all seed specialists included in the analysis.

The six species demonstrating the strongest associations between detection probabilities and snag densities and were identical to those seen in the first model (Table 4). The secondary model did provide explanations for some of the associations we saw in the first model. Still, it did not capture the complete range of change that we observed in the primary model, suggesting that many species were responding to environmental changes other than or in addition to snag density alone (Figure 14).

Table 4: $\Pr(\alpha_1 < 0)$, $\Pr(\alpha_1 > 0)$, and foraging guild for all species from the secondary model posterior distributions.

Species	Foraging Guild	$\Pr(\alpha_1 < 0)$	$\Pr(\alpha_1 > 0)$
American red tree squirrel***		0.79	
American robin	GI		0.84
American three-toed woodpecker	BI	0.91	
Barred owl	CA	0.92	
Black-capped chickadee	CI		0.81
Black-headed grosbeak	OM		0.62
Brown creeper	BI	0.74	
Brown-headed cowbird	OM	0.84	
Cassin's finch	OM	0.61	
Cassin's vireo	SI		0.95
Chipping sparrow	OM	0.94	
Clark's nutcracker*	OM	0.99	
Common raven***	OM	1.00	
Dark eyed-junco***	OM	0.86	
Downy woodpecker	BI	0.63	
Dusky flycatcher	AI	0.92	
Dusky grouse	OM		0.74
Evening grosbeak	OM	0.91	
Gray jay	OM	0.77	
Hairy woodpecker	BI	0.64	
Hammond's flycatcher	AI	1.00	
Hermit thrush***	GI	0.91	
House wren	GI	0.83	
Lazuli bunting	OM	0.69	
Lincoln's sparrow	OM		0.53
MacGillivray's warbler	SI	0.89	
Mountain bluebird	AI	1.00	
Mountain chickadee***	CI	0.70	
Mourning dove	OM	0.62	
Northern flicker	OM		0.52
Northern goshawk	CA	0.82	
Orange-crowned warbler	SI	0.10	
Pileated woodpecker	OM	0.52	
Pine siskin	OM	0.94	
Red crossbill	OM	0.70	
Red-breasted nuthatch*	BI	1.00	
Red-naped sapsucker	OM	0.85	
Red-tailed hawk	CA	0.71	
Ruby-crowned kinglet	CI	0.84	
Ruffed grouse	OM	0.90	
Steller's jay	OM	0.82	
Swainson's thrush	SI	1.00	
Townsend's solitaire***	AI	0.81	
Tree swallow	AI	0.58	

Table 4 Continued

Unidentified Empidonax flycatcher	AI	0.80
Vesper sparrow	OM	0.74
Warbling vireo	CI	0.39
Western tanager	OM	0.97
White-breasted nuthatch**	BI	0.66
Yellow-rumped warbler	CI	0.90

*** 95% CRI does not contain 0

**90% CRI does not contain 0

*85% CRI does not contain 0

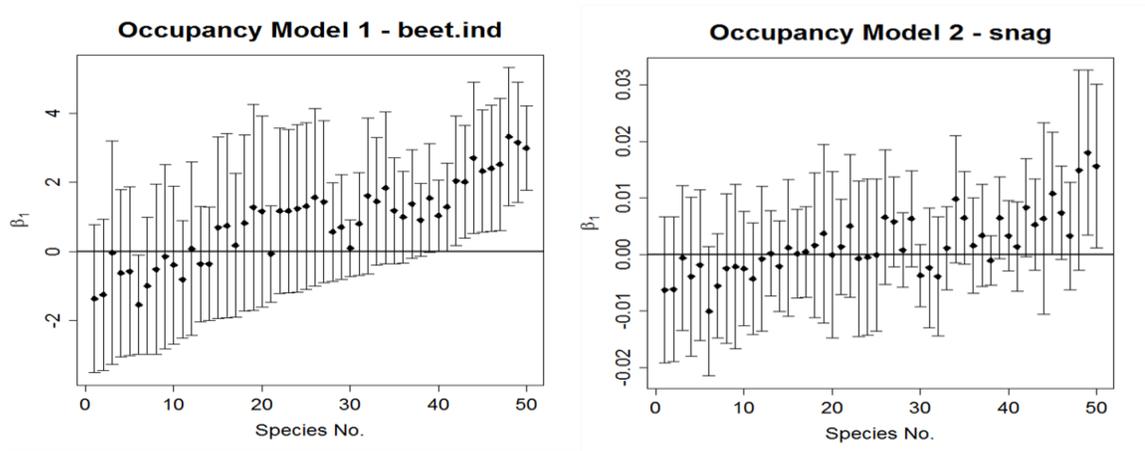


Figure 14. Comparison of β_1 estimates for primary (left) and secondary (right) models for 50 species listed in the same order. Bars represent 95% credible intervals.

Species Richness

Using the primary model, it did not appear that the mountain pine beetle epidemic strongly changed local (site-level) or global (study area-level) species richness (Figures 15 and 16). Our prediction that local species richness would increase was not met, but our prediction of constant global species richness was.

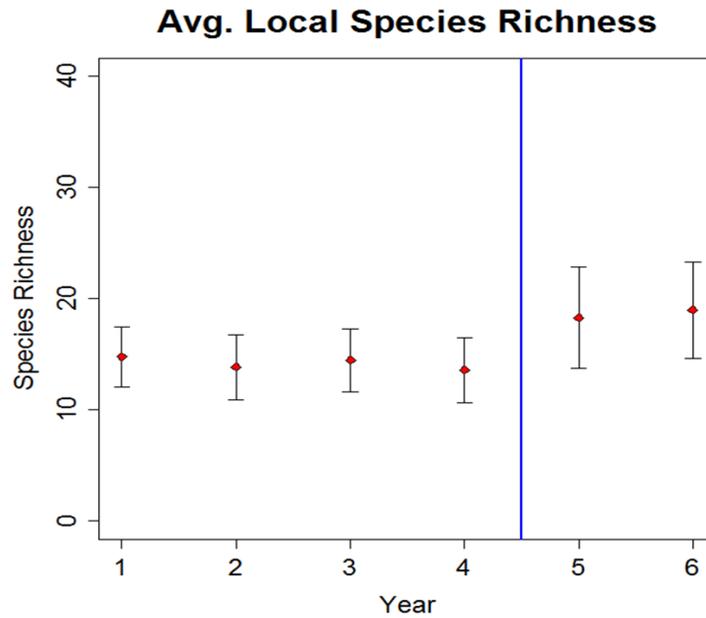


Figure 15. Estimated mean local species richness over the course of the study (based on primary model results). Bars represent 95% credible intervals. Years 1 through 4 were in the pre-epidemic period and years 5 and 6 were in during the epidemic period.

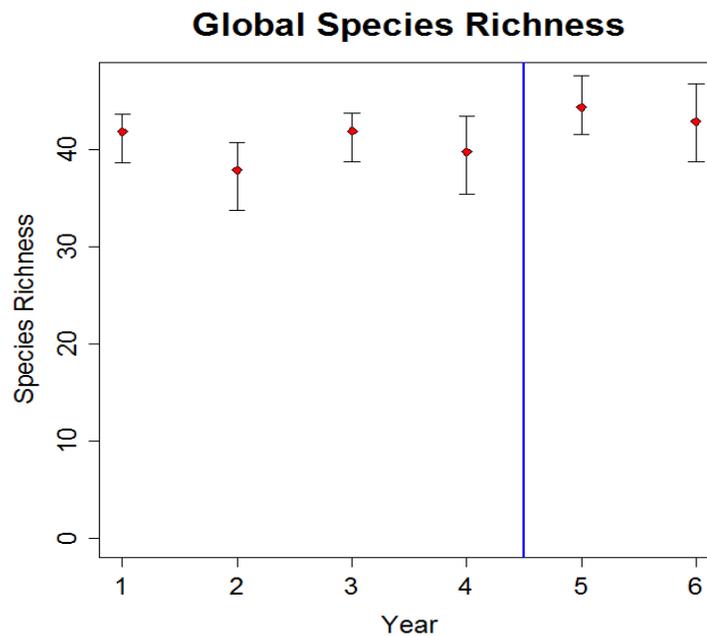


Figure 16. Estimated global species richness over the course of the study (based on primary model results). Bars represent 95% credible intervals. Years 1 through 4 were in the pre-epidemic period and years 5 and 6 were during the epidemic period.

Discussion

We found partial support for our prediction that occupancy probabilities for bark insectivores would be positively associated with the mountain pine beetle epidemic and snag density. We saw positive relationships between occupancy probabilities and these covariates for American three-toed, downy, and hairy woodpeckers but no evidence of similar associations for brown creeper, red-breasted nuthatch, and white-breasted nuthatch. This division might be related to differences in foraging strategies among these species. The American three-toed, hairy, and to a lesser extent, downy woodpeckers are all bark borers that will forage on beetle larvae. Brown creeper, red-breasted, and white-breasted nuthatches are bark gleaners and have a more generalist diet. The importance of this difference in foraging strategy is further evidenced by the fact that the woodpeckers were associated more strongly with snag density than the bark gleaners. The lack of evidence of changes in occupancy for the bark gleaning species might also be related to interspecific competition among cavity-nesting species. Territorial disputes and competition for nest trees between downy woodpecker and red-breasted nuthatch could be related to the lack of evidence we saw for changes in nuthatch occupancy probability (Martin and Eadie 1999).

Foliage-nesting and gleaning bird occupancy probabilities were predicted to have a negative relationship with the beetle epidemic and with snag density. This prediction was not well-supported. While the foliage-gleaning black-capped and mountain chickadees did show evidence of being negatively associated with the beetle epidemic and snag density, other foliage insectivores including the ruby-crowned kinglet and

warbling vireo showed positive associations. The ruby-crowned kinglet has experienced a small increase in population size over its entire North American range during the past 40 years (Butcher and Niven 2007) which might account for the unanticipated changes we saw. The warbling vireo showed a strong positive association with the beetle epidemic using the primary model, but no association with snag density in the secondary model. The last year of the study was the highest in precipitation, which is confounded within our beetle covariate (USDA NRCS: <http://www.wcc.nrcs.usda.gov>). It is likely that the warbling vireo, a deciduous associate (Gardali and Ballard 2000), experienced a positive relationship with the increase in precipitation and subsequent deciduous growth rather than the beetle epidemic.

The prediction that occupancy rates for ground- and shrub-foraging species would remain relatively constant was partially supported, as we saw no evidence of a relationship between occupancy probability and snag density (secondary model) for all members of this guild except for the shrub-foraging Swainson's thrush. In the primary model, however, we saw a positive association between the beetle epidemic and occupancy probabilities for several ground- and shrub-foraging species (American robin, house wren, MacGillivray's warbler, and Swainson's thrush). Several of these species are largely associated with aspen and willow (*Salix* spp.) thickets. The positive changes of these species might be due to the final year of the study being higher in precipitation than any other year (USDA NRCS: <http://www.wcc.nrcs.usda.gov>), which likely increased growth of deciduous aspen and willow patches. The American robin (a ground insectivore showing a positive association) is a generalist, which might explain why this

species was able to persist and even increase during the mountain pine beetle epidemic (Sallabanks and James 1999).

We found some evidence of negative associations between occupancy rates and the beetle epidemic and snag density for the pine seed specialists (Clark's nutcracker and red crossbill), though the relationship was not as strong as predicted. We expect the relationship to strengthen as we move into the post-epidemic phase. We found evidence that occupancy was positively associated with the beetle epidemic for evening grosbeak, Lincoln's sparrow, Swainson's thrush, and Pine siskin. These species are documented as predators of western spruce budworm (*Choristoneura occidentalis* Freeman), with evening grosbeak and Pine siskin exhibiting irruptive behavior (Bolgiano 2004, Torgerson and Campbell 1982, Langelier and Garton 1982, Ammon 1995). A western spruce budworm outbreak in the study area peaked in 2009 (USDA Forest Service: <http://www.fs.fed.us/r1-r4/spf/fhp/conditions/entry1.html>) and thus is confounded with the mountain pine beetle epidemic covariate in our model, but could be responsible for the strong changes observed by these species.

Snag density explained some but not all of the variation in species occupancy rates that we observed in the primary models. While snag density depicts nesting and foraging resources for cavity-nesters, it does not represent nesting resources for other guilds and might not provide an accurate portrayal of food abundances for any guild. In future modeling efforts, a model incorporating multiple metrics including mountain pine beetle abundance, downed wood density, snag density, and shrub density might provide

better inference across the entire community of small landbirds that are the focus of this study.

Both primary and secondary models identified strong negative associations between detection probability and the beetle epidemic for the same six species over the course of the study. These species (American red tree squirrel, common raven [*Corvus corax*], dark-eyed junco, hermit thrush, mountain chickadee, and Townsend's solitaire [*Myadestes townsendi*]) represent a wide range of foraging and nest guilds and the changes in detection probability identified by the model could stem from several sources. The observers conducting point count surveys in the before-epidemic and during-epidemic periods were different, resulting in a potential "observer" effect. Many of these species are fairly common however, and are not likely to be misidentified on point count surveys. Therefore, the change in detection that we noticed might in fact be related to landscape or abundance changes. Further thoughtful modeling of detection probabilities and abundances might provide further insight to this question.

In a ten-year study in British Columbia, Drever et al. (2009) linked a mountain pine beetle epidemic to increases in species richness for bark insectivores, decreases for ground insectivores, and no change (but fluctuations) for herbivores, omnivores, aerial insectivores and foliage insectivores. Our results, which focus on the short term collective changes of the entire avian community rather than foraging guilds, found little evidence of changes in species richness at either local or global scales. The lack of rapid changes to habitat alterations during the beetle outbreak might be explained by time lags created

by site tenacity of breeding birds, and suggests that ecological field studies require longer periods of post-disturbance monitoring (Wiens and Rotenberry 1985).

Scope and Limitations

Although we have contributed valuable new information to the scientific community regarding wildlife responses to insect epidemics, it is important to recognize that these results only regard short-term changes. The biologically meaningful changes in occupancy and detection rates we identified during the epidemic could be quite different than the relationships that will exist in post-epidemic conditions. For instance, dramatic changes in understory growth, downed wood, and canopy cover in the years following the epidemic (Stone and Wolfe 1996, Page and Jenkins 2007, Jenkins et al. 2008) might alter the occupancy relationships described here. Longer-term studies will also be necessary to evaluate the duration of the strong species-beetle relationships that we observed. Further study over a range of time-scales will be essential to obtaining sound understanding of the dynamic relationships between birds and beetle epidemics. In addition to using different time-scales in future studies, additional modeling techniques including abundance analyses or competing models frameworks could also be considered.

Although occupancy modeling is an excellent framework to use with point count surveys, abundance estimation is also an option. The short-term distribution responses seen in this study might be made more informative when paired with an abundance analysis. For instance, a species that was wide-ranging before the epidemic might have experienced large population declines during the epidemic, without exhibiting large

changes in area occupied. Because detection probability can act as a surrogate to abundance, the detection changes we saw in our model might in fact be related to changes in abundances for these species. Further analysis using alternative methods might provide a more complete understanding of the linkage between distribution, detection, and abundance.

Finally, the assumptions of the primary model were somewhat restrictive. This analysis should be viewed as a basic initial modeling attempt to be built upon in future modeling efforts. Incorporating year- and site-specific covariates, alternate parameterizations of colonization and extinction parameters, and potentially model selection might improve inference.

Management Implications

Mountain pine beetle outbreaks have substantial ecological and economic ramifications, and have provoked calls for policy changes of more aggressive timber harvesting and fire suppression (Raffa et al. 2008). Mountain pine beetle outbreaks increase the woody fuels and litter depth of an area in the years following a beetle epidemic (Jenkins et al. 2008), which can lead to an increased risk of wildfire (Donato et al. 2006, Anderson 1982). Concern for wildfires on public lands has provided reason for many agencies to consider salvage logging as part of their post-beetle management plans. Increased beetle outbreaks and tree mortality are expected with climate change (Bentz et al. 2010), followed by more opportunities for salvage logging (Lindenmayer and Noss 2006). Salvage logging, however, removes trees and snags that provide nesting and foraging habitat for cavity-nesting birds and other wildlife species (e.g., Lindenmayer and

Noss 2006, Saab et al. 2009). Thus, land managers face important challenges implementing post-beetle management policies, while concurrently maintaining wildlife habitat for species associated with dead trees.

This study provides essential scientific information for developing post-beetle management guidelines that maintain populations and habitats of avian species associated with dry coniferous forests following mountain pine beetle epidemics. The community-wide nature of this analysis elucidates the variety and degree of changes exhibited, and also gives managers more information upon which to base their decisions regarding post-beetle management activities. Carefully planned post-fire salvage logging prescriptions can provide habitat for successfully breeding cavity-nesting birds for at least a decade after wildfire (Saab et al 2009, 2011). We found evidence of strong relationships between snag density and breeding season occupancy probability for several species such as American three-toed, hairy, and downy woodpeckers, ruby-crowned kinglet, and Swainson's thrush. This suggests that well planned salvage operations after beetle outbreaks could also maintain suitable habitat for several successfully breeding avian species.

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APPENDICES

APPENDIX A

TABLE OF DETECTIONS BEFORE AND
DURING EPIDEMIC BY SPECIES

Appendix A. List of species common names, scientific names, American Ornithologists' Union codes, and total number of detections over entire period of study. ^aMontana Fish, Wildlife, and Parks Species of Concern. ^bHelena National Forest Management Indicator Species.

Common Name	Scientific Name	Detections Before (2003-06)	Sites with Detections Before	Detections During (2009-10)	Sites with Detections During
Ruffed grouse	<i>Bonasa umbellus</i>	0	0	1	1
Dusky grouse	<i>Dendragapus obscurus</i>	2	2	0	0
Northern goshawk	<i>Accipiter gentilis</i>	3	3	6	3
Red-tailed hawk	<i>Buteo jamaicensis</i>	6	2	5	2
Mourning dove	<i>Zenaida macroura</i>	13	10	1	1
Barred owl	<i>Strix varia</i>	2	2	0	0
Red-naped sapsucker	<i>Sphyrapicus nuchalis</i>	28	20	15	13
Downy woodpecker	<i>Picoides pubescens</i>	2	2	6	6
Hairy woodpecker	<i>Picoides villosus</i>	32	22	24	19
American three-toed woodpecker	<i>Picoides dorsalis</i>	15	11	22	19
Northern flicker	<i>Colaptes auratus</i>	5	5	5	5
Pileated woodpecker	<i>Dryocopus pileatus</i>	2	2	0	0
Hammond's flycatcher	<i>Empidonax hammondi</i>	6	4	7	7
Dusky flycatcher	<i>Empidonax oberholseri</i>	20	8	62	41
Unidentified Empidonax flycatcher	<i>Empidonax spp.</i>	7	5	0	0
Cassin's vireo	<i>Vireo cassinii</i>	75	33	25	19
Warbling vireo	<i>Vireo gilvus</i>	100	36	56	31
Gray jay	<i>Perisoreus canadensis</i>	37	31	12	11
Steller's jay	<i>Cyanocitta stelleri</i>	0	0	1	1
Clark's nutcracker	<i>Nucifraga columbiana</i>	31	24	5	4
Common raven	<i>Corvus corax</i>	13	13	10	10
Tree swallow	<i>Tachycineta bicolor</i>	0	0	1	1

Black-capped chickadee	<i>Poecile atricapillus</i>	29	25	3	2
Mountain chickadee	<i>Poecile gambeli</i>	394	75	96	55
Red-breasted nuthatch	<i>Sitta canadensis</i>	569	76	237	74
White-breasted nuthatch	<i>Sitta carolinensis</i>	24	19	5	5
Brown creeper	<i>Certhia americana</i>	39	29	17	12
House wren	<i>Troglodytes aedo</i>	0	0	6	5
Ruby-crowned kinglet	<i>Regulus calendula</i>	178	53	124	63
Mountain bluebird	<i>Sialia currucoides</i>	2	2	4	4
Townsend's solitaire	<i>Myadestes townsendi</i>	177	69	34	29
Swainson's thrush	<i>Catharus ustulatus</i>	1	1	6	6
Hermit thrush	<i>Catharus guttatus</i>	170	63	39	33
American robin	<i>Turdus migratorius</i>	125	56	83	53
Orange-crowned warbler	<i>Vermivora celata</i>	10	7	3	3
Yellow-rumped warbler	<i>Dendroica coronata</i>	487	76	206	74
MacGillivray's warbler	<i>Oporornis tolmiei</i>	15	8	24	14
Chipping sparrow	<i>Spizella passerina</i>	166	56	143	69
Vesper sparrow	<i>Pooecetes gramineus</i>	1	1	0	0
Lincoln's sparrow	<i>Melospiza lincolnii</i>	6	4	8	6
Dark eyed-junco	<i>Junco hyemalis</i>	462	75	165	71
Western tanager	<i>Piranga ludoviciana</i>	183	67	89	57
Lazuli bunting	<i>Passerina amoena</i>	7	6	0	0
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	0	0	1	1
Brown-headed cowbird	<i>Molothrus ater</i>	31	24	35	23
Cassin's finch	<i>Carpodacus cassinii</i>	0	0	2	2
Red crossbill	<i>Loxia curvirostra</i>	37	32	3	3
Pine siskin	<i>Spinus pinus</i>	77	42	112	63
Evening grosbeak	<i>Coccothraustes vespertinus</i>	20	16	70	46
American red tree squirrel	<i>Tamiasciurus hudsonicus</i>	583	76	120	64

APPENDIX B

WINBUGS MODEL SCRIPT

Appendix B. WinBUGS Code for primary model (secondary model follows same format).

```
#Brittany Mosher
#Montana State University, Dept. of Ecology
#Fall 2011

# Import covariates

#####Enter Covariates: Beetle indicator#####
#pre-beetle = 0, post-beetle = 1.
BEET.ind <- c(0,0,0,0,1,1)
UNBEET.ind <- abs(BEET.ind - 1)
is.vector(BEET.ind)

# Script to run WinBUGS community-level model for Elkhorns point count data
# Load libraries
library(R2WinBUGS)

# To help track time.
starttime <- Sys.time()

# Read in data.
dim(Data.array) # 76,4,69,5 : sites,visit,species,year, from previous script
data <- Data.array
x <- data
x[x>1] <- 1 # Make sure detection histories are 0/1.
nsite <- dim(x)[1]
nrep <- dim(x)[2]
nyear <- dim(x)[4]
nspec <- dim(x)[3]

# Assemble the data names vector for WinBUGS.
data <- list("x","nsite","nrep","nyear","nspec","BEET.ind","UNBEET.ind")

# Assemble the initial values for WinBUGS.
inits <- function (){
  list(alpha0=rep(0,nspec),alpha1=rep(0,nspec), mu.alpha0=0, mu.alpha1=0, sd.alpha0=1,
sd.alpha1=1, beta0=rep(0,nspec),beta1=rep(0,nspec), mu.beta0=0, mu.beta1=0, sd.beta0=1,
sd.beta1=1)
}

# Assemble the parameters vector for WinBUGS (What we want to track).
parameters <- c("alpha0", "alpha1", "beta0", "beta1", "BEET.psi", "UNBEET.psi", "BEET.g",
"UNBEET.g", "UNBEET.loc.rich", "BEET.loc.rich")

# Specify and save the WinBUGS model. Here it's saved to "model.txt".
# Nomenclature: j = site, k = visit, i = species, t = year
sink("model.txt")
cat("

```

```

# The model.
model{

###Model for observation process###
for(i in 1:nspec){
for(j in 1:nsite){
for(k in 1:nrep){
for(t in 1:nyear){
x[j,k,i,t] ~ dbern(pz[j,k,i,t])
pz[j,k,i,t] <- p[j,k,i,t]*z[i,j,t]

###Model for detection probability###
logit(p[j,k,i,t]) <- alpha0[i] + alpha1[i]*BEET.ind[t]
}
}
}
}

###Priors for detection probability model###
for(i in 1:nspec){

alpha0[i] ~ dnorm(mu.alpha0,tau.alpha0)
alpha1[i] ~ dnorm(mu.alpha1,tau.alpha1)
}

mu.alpha0 ~ dnorm(0,0.001)
tau.alpha0 <- 1/(sd.alpha0*sd.alpha0)
sd.alpha0 ~ dunif(0,10)

mu.alpha1 ~ dnorm(0,0.001)
tau.alpha1 <- 1/(sd.alpha1*sd.alpha1)
sd.alpha1 ~ dunif(0,10)

###Model for latent state (occupancy)###
for(i in 1:nspec){
for(t in 1:nyear){
for(j in 1:nsite){
z[i,j,t] ~ dbern(psi[i,j,t])

###Model for occupancy probability###
logit(psi[i,j,t]) <- beta0[i] + beta1[i]*BEET.ind[t]
}
}
}

###Priors for occupancy probability model###
for(i in 1:nspec){

beta0[i] ~ dnorm(mu.beta0,tau.beta0)
beta1[i] ~ dnorm(mu.beta1,tau.beta1)

}
}

```

```

mu.beta0 ~ dnorm(0,0.001)
tau.beta0 <- 1/(sd.beta0*sd.beta0)
sd.beta0 ~ dunif(0,10)

mu.beta1 ~ dnorm(0,0.001)
tau.beta1 <- 1/(sd.beta1*sd.beta1)
sd.beta1 ~ dunif(0,10)

#####Other Derived Items of Interest#####
# Occupancy rate/percent area occupied (PAO) for species(i) at time(t) in pre and post-beetle conditions
for(t in 1:nyear){
  for(i in 1:nspec){
    for(j in 1:nsite){
      Z[i,j,t] <- z[i,j,t]
      BEET.Z[i,j,t] <- Z[i,j,t]*BEET.ind[t]
      UNBEET.Z[i,j,t] <- Z[i,j,t]*UNBEET.ind[t]
    }
    BEET.psi[i,t] <- sum(BEET.Z[i,,t])/nsite
    UNBEET.psi[i,t] <- sum(UNBEET.Z[i,,t])/nsite
  }
}

##Estimated local (site) species richness
for(t in 1:nyear){
  for(j in 1:nsite){
    BEET.rich[j,t] <- sum(BEET.Z[,j,t])
    UNBEET.rich[j,t] <- sum(UNBEET.Z[,j,t])
  }
  BEET.loc.rich[t] <- sum(BEET.rich[,t])/nsite
  UNBEET.loc.rich[t] <- sum(UNBEET.rich[,t])/nsite
}

##Estimated global (regional) species richness
for(t in 1:nyear){
  for(i in 1:nspec){
    BEET.g[i,t] <- sum(BEET.Z[i,,t])
    UNBEET.g[i,t] <- sum(UNBEET.Z[i,,t])
  }
}

},fill=TRUE)
sink()

# MCMC values. Change to what works well for you. I have the iterations set low for now just to see if it
works
nc <- 3
nb <- 500
ni <- 20000
nt <- 3

```

```
# Send it all to WinBUGS and hope for the best!

#for 64bit machine
bugout <- bugs(data, inits, parameters, "model.txt", n.chains=nc, n.iter=ni,
n.burnin=nb, n.thin=nt,bugs.directory = "C:/Program Files (x86)/WinBUGS14/", debug=T)

#for 32bit machine
#bugout <- bugs(data, inits, parameters, "model.txt", n.chains=nc, n.iter=ni,
#n.burnin=nb, n.thin=nt,debug=T)

endtime <- Sys.time()
runtime <- endtime - starttime
runtime

# Clean up:
rm(nc, nb, ni, nt, nsite, nrep, nspec, nyear, data, inits, parameters,x, starttime,endtime,runtime)

#use bugout object to manipulate results in R environment
```