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Dear Rick:

Enclosed is the final report for “Coon Creek revisited: wildlife responses to beetle-caused tree death”, Cooperative Agreement Number 09-CS-11020600-043. Submission of this document fulfills the final reporting requirement for this project. The report includes two peer-reviewed journal articles: 1) “Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests” published in *Forest Science* (2013), and 2) “Tree mortality after synchronized forest insect outbreaks: effects of tree species, bole diameter, and cutting history” published in *Forest Ecology and Management* (2014). We also include a manuscript nearing submission for peer-review, “Climate-associated forest mortality interacts with timber harvest to influence population dynamics of a vertebrate seed predator”, and figures illustrating changes in relative abundance for 13 avian species commonly associated with subalpine forest during 1985-1996, and 2011-2012. It is our intention to submit manuscripts based on these avian data sets over the next 1-2 two years.

Located in the Sierra Madre Range of south-central Wyoming, the Coon Creek study site, comprising the Coon Creek and adjacent East Fork, Encampment River (East Fork) watersheds was the site of a water yield augmentation project begun in 1985 and completed in 1996. The study was primarily intended to evaluate the efficacy of timber harvest techniques to increase surface water yield at the scale of large basins. The paired watersheds covering 1673 ha (Coon Creek) and 908 ha (East Fork) were selected based on similar size, aspect, elevation, and timber cover. During 1990-1992, 240 small patch cuts (1.2-4 ha) were created in Coon Creek while the East Fork remained untreated. Prior to harvest, both watersheds were dominated by lodgepole pine (~60%) and Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*; ~40%), and ~70% of the forest was categorized as mature.

The patch-cutting treatment was expected to result in forest perforation, and an additional study was initiated to monitor effects of timber harvest on wildlife. Data on bird, small mammal, and American marten (*Martes americana*) populations were collected during 1985-1996 by researchers at the Rocky Mountain Research Station, USDA Forest Service, in collaboration with the University of Wyoming. Wildlife was sampled across both watersheds before and after the cutting treatment, resulting in data collected over 12 years.

Beginning in approximately 1996, mountain pine beetle (MPB: *Dendroctonus ponderosae*) populations erupted in north-central Colorado and south-central Wyoming. Since approximately 2005, MPB populations have been at epidemic levels in mountains of southern Wyoming. As of 2012, over 1.7 million ha of pine (*Pinus* spp.) – dominated forests in south-central Wyoming and Colorado had been affected by this outbreak. Additional outbreaks of other bark beetle species occurred concurrently with the initial MPB outbreak. These species include spruce beetle (*Dendroctonus rufipennis*), the outbreak of which began with a large blowdown event in 1997 near Steamboat Springs, Colorado, and western balsam beetle (*Dryocoetes confusus*), a species implicated in subalpine fir decline and first reported in Wyoming in 1999. The occurrence of these roughly synchronized bark beetle outbreaks at the Coon Creek study site where pre-outbreak data on wildlife and forest structure and composition were collected presented the opportunity to evaluate wildlife responses to the beetle outbreaks, and whether patch-cutting influenced tree mortality. Data collection resumed during 2010-2012, and principal investigators included Steve Buskirk (University of Wyoming) and Greg Hayward (USDA Forest Service).

All data collected during this study were transferred to USDA Forest Service personnel (Richard Truex, Region 2) as of 31 December 2012. These data included all historical data (1985-96) from point count surveys, vegetation surveys, and small mammal trapping efforts, as well as contemporary data (2010-12) from point count, vegetation, bark-foraging bird, and midden surveys. All sampling during 2010-12 occurred at locations established during 1985-1996, so no new maps or spatial data were created for the Coon Creek study site. The sampling points were permanently marked with numbered re-bar stakes, so that each point can now be located for decades to come.

Please let us know if there are any further data that we can provide to you that would be useful in completing this reporting process. We will continue to provide you with updates on the publication status of various avian data sets. It has been a pleasure to collaborate with you and other Forest Service biologists over the last few years. We have appreciated the opportunity to be involved in this important project.

Regards,
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Ecological Consequences of Mountain Pine Beetle Outbreaks for Wildlife in Western North American Forests

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Mountain pine beetle (*Dendroctonus ponderosae*) (MPB) outbreaks are increasingly prevalent in western North America, causing considerable ecological change in pine (*Pinus* spp.) forests with important implications for wildlife. We reviewed studies examining wildlife responses to MPB outbreaks and postoutbreak salvage logging to inform forest management and guide future research. Our review included 16 studies describing MPB outbreak relationships with 89 bird species and 6 studies describing relationships with 11 mammalian species, but no studies of reptiles or amphibians. We included studies that compared wildlife response metrics temporally (before versus after the outbreak) and spatially (across sites that varied in severity of outbreak) in relation to beetle outbreaks. Outbreaks ranged in size from 20,600 to $\geq 10^7$ ha and studies occurred 1–30 years after the peak MPB outbreak, but most studies were conducted over the short-term (i.e., ≤ 6 years after the peak of MPB-induced tree mortality). Birds were the only taxa studied frequently; however, high variability existed among those studies to allow many inferences, although some patterns were evident. Avian studies concluded that cavity-nesting species responded more favorably to beetle-killed forests than species with open-cup nests, and species nesting in the shrub layer favored outbreak forests compared with ground and open-cup canopy nesters that generally showed mixed relationships. Bark-drilling species as a group clearly demonstrated a positive short-term association with MPB epidemics compared with that of other foraging assemblages. Cavity-nesting birds that do not consume bark beetles (i.e., secondary cavity-nesting species and nonbark-drilling woodpeckers) also exhibited some positive responses to MPB outbreaks, although not as pronounced or consistent as those of bark-drilling woodpeckers. Mammalian responses to MPB outbreaks were mixed. Studies consistently reported negative effects of MPB outbreaks on red squirrels (*Tamiasciurus hudsonicus*). However, there is evidence that red squirrels can persist after an outbreak under some conditions, e.g., when nonhost tree species are present. For small mammal species associated with forest understories, responses may be most pronounced during the postepidemic period (>6 years after the peak of beetle-induced tree mortality) when snags fall to produce coarse woody debris. Postoutbreak salvage logging studies ($n = 6$) reported results that lacked consensus. Postoutbreak salvage logging may have an impact on fewer wildlife species than postfire salvage logging, probably because only host-specific tree species are removed after beetle outbreaks.

Keywords: bark beetles, *Dendroctonus*, disturbance, salvage logging, wildlife

Forest landscapes of western North America are structured by complex interactions of climate, topography, soils, and disturbance. They are shifting mosaics whose vegetation reflects variation in disturbance frequency, severity, and time since disturbance ranging from years to centuries (Peet 2000). Many disturbance regimes have been altered since Euro-American settlement due to fire suppression, logging, grazing, and climate change (e.g.,

Agee 1993). After decades of fire suppression and even-aged management of forests followed by climate warming, elevated tree densities in many forests have increased the likelihood and size of mountain pine beetle (*Dendroctonus ponderosae*) (MPB) outbreaks (Taylor et al. 2006). More generally, multiple outbreaks of several bark beetle species have caused widespread tree mortality in conifer forests since the early 1990s in western North America (Raffa et al.

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2008). Severe outbreaks spanning thousands of hectares (hereafter referred to as “large-scale”) have focused public attention on the risks (e.g., hazard trees and fire, especially in the wildland-urban interface) and landscape changes posed by bark beetles. Importantly, the MPB plays an ecosystem role by principally attacking old or weakened trees, allowing younger trees to develop, while providing an important food resource to insectivores such as woodpeckers. Nonetheless, beetle outbreaks cause considerable ecological change in pine forests with important implications for wildlife populations and habitat (Drever and Martin 2007).

The impacts of MPB outbreaks on forest vegetation, a major component of wildlife habitat, are well documented and easily observed. The principal result of an outbreak is widespread tree mortality across large contiguous areas, comparable to the effects of other large-scale disturbances such as wildfire. Beetle outbreaks occur over multiple years, however, and only affect certain tree species. Similarly, the effects of MPB outbreaks on wildlife populations also vary among species and forest types. These effects must be considered within a spatiotemporal context that includes the time since outbreak, the outbreak severity, and the spatial pattern of the outbreak (e.g., large, homogeneous stands of affected trees versus patchy distributions). Dense, even-aged forest stands are considered more susceptible to bark beetle attacks than open-grown stands (Sartwell and Stevens 1975, Mitchell et al. 1983). Lodgepole pine (*Pinus contorta*) landscapes in western North America are typically composed of dense, even-aged stands often maintained by infrequent, high-severity fires (Schoennagel et al. 2004). As a result, large, contiguous landscapes of lodgepole pine have become simultaneously more susceptible to bark beetle outbreaks than landscapes dominated by ponderosa pine (*Pinus ponderosa*) (Chapman et al. 2012). Ponderosa pine forests are characterized by both low-severity fires and patches of high-severity fires, creating a more diverse, uneven-aged landscape mosaic that is less favorable to MPB outbreaks across broad regions (Sherriff and Veblen 2007). Tree mortality rates and, consequently, the recruitment of snags and downed wood may be higher in forests more susceptible to MPB outbreaks (i.e., lodgepole pine), probably affecting habitat for wildlife differently than outbreaks in less susceptible forests (i.e., ponderosa pine).

A diverse array of vertebrate species depend on forest vegetation maintained by large-scale disturbances of beetles and fire in western North America. Forest managers require a thorough understanding of the variability inherent in the region’s disturbance regimes, as well as associated population and distributional changes in vertebrate fauna, to make decisions about maintaining functioning ecosystems. Compared with other natural and managed disturbances, such as wildfire, prescribed fire, and timber management (e.g., Hobbs and Spowart 1984, Saab and Powell 2005, Russell et al. 2009a), little is known about wildlife responses to large-scale insect epidemics (Martin et al. 2006). In addition, many forest managers are faced with decisions about salvage logging of beetle-killed forests. Salvage logging removes dead and weakened trees, which may exacerbate the negative impacts of beetle outbreaks on both landscape structure and wildlife populations (Lindenmayer et al. 2008). With a changing climate (Bentz et al. 2010), increased tree mortality from both insects and fire will create more opportunities for salvage logging (cf. Lindenmayer and Noss 2006, Saab et al. 2011). Thus, land managers face significant challenges in implementing management policies for beetle- and fire-killed forests, while concurrently maintaining habitat for focal wildlife species associated with dead trees.

Bark beetle-caused tree mortality provides important habitat for wildlife that depend on snags and downed logs by providing nesting, roosting, and foraging substrate (e.g., Drever and Martin 2007). Bark beetle larvae followed by strong pulses in wood-boring and other insects can increase food supplies for some species, notably woodpeckers (e.g., Bonnot et al. 2009). Downed logs potentially benefit some species (e.g., woodpeckers and small mammals) by increasing insect availability to forest floor dwellers (e.g., carpenter ants) (Bull et al. 2007) or creating refugia from predators; however, logs could adversely affect movement of other species (e.g., elk [*Cervus canadensis*] and deer [*Odocoileus* spp.]) (Light and Burbridge 1985). Other negative effects of beetle outbreaks on wildlife include loss and desiccation of pine needles needed for nesting and foraging substrate and loss of hiding cover and mature tree habitat crucial for some wildlife species (e.g., American marten [*Martes americana*]) (Steventon and Daust 2009, Mosher 2011). Such changes in vegetation structure could result in increased vulnerability to predation or weather-caused mortality. In addition, loss of cone-producing trees can result in decreased abundance of conifer seed predators (Koprowski et al. 2005, Barringer et al. 2012).

After the postepidemic stage of beetle outbreaks, increased soil nitrogen potentially results in large increases in understory shrub and herbaceous vegetation (Stone and Wolfe 1996, Page and Jenkins 2007, Jenkins et al. 2008). Such changes can benefit wildlife species associated with early seral vegetation (cf. Hannon and Drapeau 2005). Wildlife responses to beetle-killed forests will depend on the severity and size of the outbreaks, the time since outbreak, and the conditions before the outbreak and the spatial context in which the outbreak occurs. The variation in outbreak characteristics among forest types (e.g., lodgepole-dominated versus ponderosa-dominated forests) may translate into further variability in wildlife responses.

In this article, we summarize studies investigating wildlife responses to MPB outbreaks to inform forest management decisions and identify knowledge gaps to guide future research. We reviewed studies examining the demographic responses of vertebrates to temporal (before versus after) and spatial (outbreak versus no outbreak) changes in forest conditions as a result of MPB outbreaks. Our review necessarily focuses on wildlife responses to outbreak events in lodgepole and ponderosa pine forests because only these forest types were represented in the literature quantifying wildlife relationships. We do, however, discuss other pine systems (e.g., whitebark pine [*Pinus albicaulis*]) to the extent allowed by the literature and point out knowledge gaps associated with still other systems. We also review published results describing wildlife associations with post-outbreak salvage logging. Because published studies were sparse, we supplemented our literature review with analyses of three novel data sets describing wildlife associations with MPB outbreaks.

Methods

Literature Review

We conducted a comprehensive search for studies relating terrestrial wildlife (vertebrate) population responses to MPB outbreak. We relied primarily on Google Scholar to search for both peer-reviewed and gray literature. We selected search terms from two sets. Set 1 consisted of bark beetle, mountain pine beetle, and *Dendroctonus*. Set 2 consisted of wildlife, vertebrates, birds, mammals, reptiles, amphibians, woodpeckers, *Picoides*, cavity-nesting birds, ungulates, rodents, squirrels, Sciuridae, and American marten. We used every possible pair of terms consisting of one member from set

1 and the other from set 2. We also conducted searches with all possible combinations of three terms: one from set 1, the second as either wildlife or vertebrates, and the third as salvage logging, to find studies specifically documenting wildlife responses to postoutbreak salvage logging. We scanned article titles to identify studies documenting demographic (e.g., abundance and fitness components) or ecological (i.e., habitat use) relationships with outbreaks or postoutbreak salvage logging. We considered studies that examined either temporal (before-after comparisons or trend analyses across pre- and postoutbreak or salvage years) or spatial (relationships between outbreak versus no outbreak and logging intensity) responses. We excluded studies presenting only postoutbreak results from beetle-affected areas and studies focusing solely on the effects of MPB outbreaks or salvage logging on wildlife habitat attributes. We focused on studies of wildlife (terrestrial vertebrates) responses to MPB outbreaks. As such, our review centered on western North America (i.e., the range of the MPB) and excluded wildlife relationships with beetle populations at endemic levels.

We summarized population responses as positive (increases in abundance or productivity with outbreak conditions or selection for beetle-affected habitats), negative, mixed (variable among years or study sites), or not statistically significant for each study. We did not conduct a formal meta-analysis because of the paucity of published data, variability in metrics evaluated, and lack of statistics in some studies. When provided, we deferred to authors' assessments of statistical significance (e.g., thresholds for *P* values from formal statistical tests or extent of overlap of confidence [frequentist analyses] or credible intervals [Bayesian analyses] for relevant model parameters). When authors provided estimates of population responses with confidence intervals (CIs) but did not explicitly assess statistical support for responses by certain species, we considered responses significant if 95% of the probability mass for the response parameter estimate lay above or below zero. If authors did not conduct any statistical analyses (e.g., compared mean encounter rates without CIs), we subjectively assessed whether differences among sites or years appeared substantial while also recording which studies lacked statistical analysis to inform inferences made by the reader.

Avian Responses to MPB Outbreaks

We focused our review of avian literature on species-specific responses to MPB outbreaks or postoutbreak salvage logging. In addition, we reported community-level metrics (e.g., species richness and diversity indices) for studies that included species-specific responses. Our review focused on forest-associated species and therefore excluded most aquatic species except those relying on tree cavities for nesting. We organized our synthesis using an assemblage approach rather than attempting to examine individual responses of nearly 100 vertebrate species (cf. Saab and Powell 2005). We looked for assemblage-level patterns that appeared consistent across studies. We expected wildlife responses to MPB outbreaks to be modulated by species-specific ecological or life history traits. Our approach allowed insights into mechanisms underlying wildlife species relationships with MPBs.

We summarize our a priori directional predictions of assemblage-level responses to MPB outbreak conditions in Table 1. Because of their reliance on snags for both nesting and foraging (snag-associated invertebrates), we expected beetle-foraging woodpeckers, particularly *Picoides* spp., to respond positively. In particular, American three-toed (*Picoides dorsalis*) and black-backed (*Picoides arcticus*) woodpeckers are disturbance specialists; thus, we expected these

Table 1. Expected responses by vertebrate assemblages to large-scale (thousands of ha), recent MPB outbreaks (≤ 6 years after the peak of beetle-caused tree mortality).

| Assemblage | Expected response |
|--|--|
| Avian | |
| Cavity-nesting: beetle foraging ¹ | Strongly positive because of increases in nesting and foraging substrates. |
| Cavity-nesting: non-beetle foraging ² | Moderately positive because of increases in nesting substrate. |
| Shrub-nesting: ground insectivores | Neutral because of few changes in ground and shrub vegetation. |
| Canopy-nesting: foliage insectivores | Strongly negative because of desiccation of nesting and foraging substrates. |
| Canopy-nesting: pine seed consumers | Moderately negative because of loss of pine seed production. |
| Mammalian | |
| Cavity/snag-reliant | Positive because of increases in roosting/denning substrate. |
| Early seral associates | Moderately positive because of early seral vegetation |
| Pine seed consumers | Negative because of losses of pine seed production. |

Assemblages are broadly grouped by nesting/foraging mode for avian groups and by habitat/foraging associations for mammalian groups.

¹ Referenced as bark-drilling insectivores in Table 3.

² Includes all non-bark-drilling woodpeckers and secondary cavity nesters listed in Table 3.

species to exhibit the most consistently positive responses. More generally, we expected cavity-nesting birds to respond positively. Cavity excavators were expected to benefit from increased availability of snags, which facilitate excavation (Martin and Eadie 1999), and secondary cavity nesters were expected to respond positively to the increased availability of cavities provided by the excavators (Norris 2012, Norris et al. 2013). However, we expected cavity-nesting, bark-gleaning insectivores to have a weaker response than beetle-foragers because these species (e.g., brown creeper [*Certhia americana*] and red-breasted nuthatch [*Sitta canadensis*]) often nest in snags but rely primarily on live trees as a foraging substrate (Ghalambor and Martin 1999, Hejl et al. 2002).

Minimal short-term changes (< 6 years after outbreak peak) in ground and shrub vegetation are expected during beetle epidemics (Jenkins et al. 2008). Immediately after the postepidemic stage (>6 years after the peak in beetle-induced tree mortality); however, large increases in understory shrub and herbaceous vegetation can occur (Stone and Wolfe 1996, Page and Jenkins 2007, Jenkins et al. 2008). Consequently, we expected shrub-nesting species and ground insectivores to exhibit a lagged positive response paralleling an expected lagged growth of shrubs in response to decreased canopy cover, similar to successional changes after wildfire (Hannon and Drapeau 2005). In addition, we expected foliage insectivores, canopy-nesting species, and pine seed consumers that rely heavily on live pine trees for food to respond negatively to large-scale outbreak conditions. We also anticipated inconsistent to nonexistent responses in species richness and total bird abundance because of variation in species' life history requisites.

Because of differing MPB-related disturbance regimes in lodgepole pine-dominant versus ponderosa pine-dominant forests, we expected differences in wildlife responses between the two forest types. Lodgepole pine landscapes are typically maintained by infrequent, high-impact disturbance events, resulting in dense, low-diversity stands that are more susceptible to insect outbreaks than ponderosa pine forests (Sherriff and Veblen 2007, Chapman et al. 2012). Larger and more severe outbreaks could result in stronger

responses (both positive and negative) by wildlife. Thick bark and sapwood make ponderosa pine trees particularly valuable for nest excavation and foraging by cavity-nesting birds and bark insectivores (Bull et al. 1997, Saab et al. 2009). Thus, one might expect more positive responses by these groups to MPB outbreaks in ponderosa pine-dominated forests.

Novel Data: Woodpecker Nest Survival and Densities in Western Montana To augment the review, we present new data on woodpecker demographics before and after a MPB outbreak. We studied nest survival and nest densities of five woodpecker species in relation to a MPB outbreak in western Montana, USA. (46°28' N, 111°52' W). The forest was characterized as dry mixed conifer dominated by ponderosa pine with lesser amounts of lodgepole pine and Douglas-fir, interspersed with aspen (*Populus tremuloides*) patches (Mosher 2011). As accompaniment to our outlined expectations (Table 1), we specifically predicted that nest survival and nest densities of bark-drilling specialists (American three-toed woodpecker [*P. dorsalis*]), hairy woodpecker [*Picooides villosus*], and downy woodpecker [*Picooides pubescens*]) would increase in relation to the MPB outbreak due to increased food resources (i.e., beetle larvae), increased nesting substrate (i.e., conifer snags), and decreased nest predation by red squirrels (*Tamiasciurus hudsonicus*) (e.g., Leonard 2001, Jackson and Ouellet 2002, Jackson et al. 2002, Mosher 2011, Saab et al. 2011). In contrast, we expected fewer changes in nest survival or densities for species that infrequently feed on bark beetle larvae and favor aspen trees for nesting (red-naped sapsucker [*Sphyrapicus nuchalis*] and Northern flicker [*Colaptes auratus*]) (e.g., Moore 1995, Walters et al. 2002).

We searched for and monitored woodpecker nests using standard methods (Dudley and Saab 2003) in four units of approximately 250 ha in size that were selected by the Helena National Forest for restoration treatment before the outbreak (Mosher 2011). We monitored for 4 years (2003–2006) before and 3 years (2009–2011) after the peak in beetle-caused tree mortality (B.J. Bentz, USDA Forest Service, unpubl. data, Logan, UT, 2011). Nests were monitored every 3–4 days until nest fate could be determined as either successful or failed. We estimated nest survival rates before and after the beetle outbreak by calculating the probability of daily nest survival (Mayfield 1975), assuming constant daily survival rates within the two time periods. We calculated SEs and 95% CIs (Johnson 1979) to compare nest survival rates between periods. Although we did not correct for detection probabilities, survey area and effort were equivalent before and after the outbreak, yielding information on relative nest densities. We measured the linear relationship between nest densities and year using a Pearson correlation coefficient. We expected nest densities to change positively with year during the outbreak because of increases in nesting substrate (i.e., snags) and in food resources (i.e., beetle larvae). We also used a *t* test to examine statistical differences in nest densities before and after the peak in beetle-caused tree mortality.

Nonavian Responses to MPB Outbreaks

Our review of the literature on nonavian species' responses to MPB outbreaks and subsequent salvage logging focused on species-level responses. We expected mammals relying on cavities or snags to benefit in the short-term (≤ 6 years after peak of tree mortality) by MPB outbreaks. Similarly, for species that use coarse woody debris for resting and winter survival, such as fishers (*Martes pennanti*), American marten, and small mammals (e.g., voles [*Clethrionomys* spp.] and chipmunks [*Tamias* spp.]), we expected positive responses

to MPB outbreaks in the longer-term (> 6 years after peak tree mortality), unless postoutbreak salvage logging occurs (Powell and Zielinski 1994, Steventon and Daust 2009). We also expected species closely associated with early seral habitats, such as deer and elk, to respond positively to the postepidemic period with a time lag, allowing for increases in herbaceous and shrub growth. We expected nonavian species that rely on pine seeds as key forage items, such as grizzly bears (*Ursus arctos*) or red squirrels, to be negatively affected by MPB outbreaks.

Novel Data: Red Squirrel Occurrence in Southern Wyoming We studied red squirrel occurrence in relation to a MPB outbreak in two adjacent watersheds, the East Fork of the Encampment River (East Fork: 911 ha) and Coon Creek (1,615 ha), located in the Sierra Madre Range of Southcentral Wyoming (41°03' N, 106°43' W). Both watersheds were dominated by lodgepole pine (60%) with Engelmann spruce (*Picea engelmannii*)-subalpine fir comprising slightly less forest cover (40%). Both watersheds were characterized as approximately 70% mature forest in 1985 (Raphael 1988). A MPB epidemic began at the site in 1996, and spruce beetles became active beginning in 1997 (Harris et al. 2001). Mortality rates of lodgepole pine and Engelmann spruce > 30 cm dbh were 60–100% depending on size class, respectively (T. Johnson, University of Wyoming, unpubl. data, 2012).

Fixed radius point counts were conducted for red squirrels at 90 sampling points in each watershed ($n = 180$). Sampling points were distributed along eight variable-length transects in each watershed, with points along a transect 200 m from each other and transects spaced 400 m apart. Each point was visited five times in 2011 and six times in 2012 between dawn and 11:00 am MST. All red squirrels seen or heard within 50 m were recorded. We quantified stand basal area in July–August 2011 at each sampling point using a prism and measured separately for live and dead trees of all species. More details regarding the study site and sampling design were reported by Raphael (1988).

Given the low number of squirrel detections at each sampling point (usually ≤ 1), we focused our analysis on squirrel occurrence rather than abundance. To evaluate the relationship between red squirrel occurrence and tree mortality, we used logistic regression (Program R, version 2.15.2). Our regression model included three predictor variables and described the probability of a red squirrel being observed within 50 m of a sampling point. Regression models did not account for detectability. Models therefore estimated the unconditional probability of observing a squirrel, which is a function of both occurrence and detectability (MacKenzie et al. 2002). Consequently, we considered the potential influence of detectability when interpreting our results. We used live basal area as an index to beetle-killed tree mortality because we expected red squirrel occurrence to be related to the number and size of live cone-bearing trees. Squirrels at our study site consumed seeds of lodgepole pine, spruce, and fir (T. Johnson, University of Wyoming, unpubl. data, 2012); thus, we expected squirrel occurrence to be positively related to total live basal area of all three species. We also included watershed as a predictor variable to control for historical variation in levels of timber harvest between watersheds (Troendle et al. 2001) and year to control for interannual environmental variation and variation in observers. Although we did not account for the potential effects of detection probability, we expected that differences in red squirrel detection would manifest as a watershed effect because of differences in average live basal area between watersheds (i.e., Coon Creek [5.7 ± 0.4 m²/ha (mean \pm SE)] versus East Fork [7.7 ± 0.4

m²/ha]). We used the Le Cessie-van Houwelingen normal test statistic for unweighted sum of squared errors to test model fit to the data (Le Cessie and Van Houwelingen 1991). We considered $P > 0.05$ to indicate adequate fit.

Novel data: Southern Red-Backed Vole Density in Southern Wyoming

We examined the density of the southern red-backed vole in relation to MPB-caused mortality of lodgepole pine and Engelmann spruce mortality (caused by the spruce beetle, *Dendroctonus rufipennis*) during 2010–2011. The southern red-backed vole is a common tenant of North American subalpine forests, a critical disperser of mycorrhizal fungal spores, and the primary prey for several species of forest mesocarnivores (Keinath and Hayward 2003). Our study area was the Snowy Range of Wyoming (Medicine Bow National Forest; 41°30' N, 106°29' W), an area recently (2003–2009) affected by a large-scale MPB epidemic. Focal forest patches ($n = 38$) ranged in size from 7.5 to 220 ha and comprised Engelmann spruce, subalpine fir, and lodgepole pine between 2,700 and 3,100 m in elevation. Stands dominated by mature lodgepole were already largely dead from MPB infestation at the time of study initiation in 2010 (Collins et al. 2011). Our focal patches contained some live mature trees and represented variation in the extent of beetle-induced tree mortality.

We live-trapped voles using Sherman traps during August–September 2010–2011. We established a single trap grid within each forest patch at a random location and standardized distance (50 m) from patch edges to control for potential edge effects (Fletcher et al. 2007). Each grid consisted of 60 traps spaced 10 m apart. Traps were baited with peanut butter, bird seed, oatmeal, and green apple for hydration and deployed for 4 consecutive nights. We marked each captured animal with a passive integrated transponder tag. Percent mortality of mature lodgepole pine, spruce, and fir trees was quantified by counting trees within 2–3 m (depending on relative tree density) of transects and dividing the number of dead trees by the total number of trees of each species. Further methodological details are reported by Hayward (2012).

Abundance estimates (\hat{N}) for each trapping session were calculated in Program MARK (version 6.2; White and Burnham 1999) using the closed population model. No individuals were captured in more than 1 year so we estimated abundance separately for each patch and each year. Capture and recapture probabilities were allowed to vary among trapping sessions. For grids with fewer than seven unique captures, we first used the minimum number of individuals known alive (MNKA), a count of the number of unique individuals captured at each grid, to calculate naive abundance estimates for each patch. We then regressed the MNKA values against the corresponding \hat{N} estimates and used the regression coefficients to calculate final abundance population estimates. Densities were estimated by calculating the effective trapping area based on the mean of the maximum distance moved by recaptured individuals (Tioli et al. 2009), which yielded an effective trap area of 1.82 ha. Density estimates from patches trapped during both years ($n = 8$) were averaged. Densities were compared using linear regression with patch size (ha), percent lodgepole mortality, and percent spruce mortality as predictors.

Results

Avian Relationships with MPB Outbreaks

We reviewed 16 studies (11 peer-reviewed) examining responses of 89 species to MPB outbreaks, of which 65 species were open-cup nesters and 24 were cavity-nesting species (Table 2). Most studies

were conducted in mixed conifer forests with a lodgepole component and were designed to assess spatial relationships (i.e., differences between outbreak versus no-outbreak sites or relationships with spatial variation in outbreak severity; $n = 7$ studies). No study specifically examined the effect of outbreak size on vertebrate responses. Limited sampling in a wide range of outbreak sizes prevented meaningful inference about the influence of outbreak size on wildlife responses (Table 2).

Relatively few studies were designed to evaluate temporal relationships (i.e., before-after comparisons; $n = 6$ studies), and only 3 were both spatial and temporal associations (Table 2). Most studies were conducted during the early epidemic period (≤ 6 years after peak in beetle-induced tree mortality), whereas only two were conducted during the postepidemic phase (Bull et al. 2007, Edworthy et al. 2011).

Studies primarily assessed outbreak relationships with some sampled measure of population status (e.g., relative or absolute abundance or density or site occupancy rates) (Table 3). Six studies evaluated other types of ecological relationships (nest site selection, clutch size, nest survival, and population growth) by nine cavity-nesting species (seven woodpecker species, red-breasted nuthatch, and mountain chickadee [*Poecile gambeli*]). Statistically significant positive relationships (based on increases in abundance, occupancy, or productivity metrics with outbreak conditions or selection for beetle-affected habitats) were reported for 36 species, and studies lacking statistics reported apparent positive associations for two more species (total 38). Statistically significant negative relationships were reported for 18 species, and studies lacking inferential statistics reported apparent negative associations for six more species (total 24).

Most studies (11 of 16) reported woodpecker relationships with MPB outbreaks. Six of eight woodpecker species, including four *Picoides* spp., exhibited positive relationships, whereas only two species (Northern flicker [*Colaptes auratus*] and red-naped sapsucker [*Sphyrapicus nuchalis*]) exhibited negative relationships. Of the two disturbance specialists, the American three-toed woodpecker demonstrated positive relationships in a majority of studies, whereas the black-backed woodpecker also exhibited a positive relationship, but only in one of five studies. The Northern flicker exhibited mixed associations (negative and positive) with MPB outbreaks. Woodpecker species classified as omnivores tended to exhibit nonsignificant or negative relationships in a greater proportion of studies than did bark-drilling specialists (excepting black-backed woodpeckers [*P. arcticus*]).

Studies documented significant positive relationships for 12 cavity-nesting species (six excavator, one facultative excavator, and five nonexcavator species). Negative relationships were documented for six cavity-nesting species (two excavators, one facultative excavator, and three nonexcavators). Four cavity-nesting species (one facultative excavator [red-breasted nuthatch], and three nonexcavators [mountain chickadee, winter wren (*Troglodytes hiemalis*), and brown creeper] exhibited variable relationships. Seven species of cavity nesters (six nonexcavator species and one excavator) did not show a significant or apparent relationship.

Reviewed studies presented data on four bark-gleaning species for which variable relationships were documented (Table 3). Brown creepers exhibited positive, mixed, and no relationship, depending on the study. Red-breasted nuthatch showed primarily positive relationships.

Table 2. Studies reviewed for wildlife relationships with MPB outbreaks and with postoutbreak salvage logging.

| No. | Reference | Location | Outbreak timing | Veg | Study years | Outbreak size (ha) | Design |
|-----|---|----------|------------------------|-----|----------------------|-----------------------------------|----------------------|
| 1 | Bonnot et al. 2008 ^{PR,MPB,A} | SD | 1998–2004 | MP | 2004–2005 | 27,000 | Spatial |
| 2 | Bonnot et al. 2009 ^{PR,MPB,A} | SD | 1998–2004 | MP | 2004–2005 | 27,000 | Spatial |
| 3 | Bull 1983 ^{PR,MPB,A} | OR | Early 1970s | L | 1976 | 200,000 | Spatial |
| 4 | Bull et al. 2007 ^{PR,MPB,A} | OR | Early 1990s | MP | 1973–2005 | Not reported | Temporal |
| 5 | A. Chalfoun and J. Heyward, unpubl. data, 2012 ^{MPB,N,M} | WY | 2003–2009 | ML | 2010–2011 | 1.6 × 10 ⁶ | Spatial |
| 6 | Chan-McLeod et al. 2008 ^{MPB,A} | BC | 1999–2004 | ML | 2004–2005 | Not reported | Spatial |
| 7 | Cichowski 2010 ^{MPB,M} | BC | Pre-2001 | M | 2006–2009 | Not reported | Spatial |
| 8 | Drever and Martin 2007 ^{MPB,A,M} | BC | Peaked 2003 | M | 1995–2004 | 8.5 × 10 ⁶ | Temporal |
| 9 | Drever and Martin 2010 ^{PR,MPB,S,A} | BC | Peaked 2003 | M | 1997–2008 | ≥10 ⁷ | Temporal and spatial |
| 10 | Edworthy et al. 2010 ^{PR,MPB,S,A} | BC | Peaked 2003 | M | 1995–2009 | ≥10 ⁷ | Temporal |
| 11 | T. Johnson and S. Buskirk, unpubl. data, 2012 ^{MPB,N,M} | WY | 1996–2012 | ML | 2011–2012 | East Fork: 911; Coon Creek: 1,615 | Spatial |
| 12 | Kroll et al. 2012 ^{PR,S,A} | OR | 1980s | M | 1996–1998 | 250,000 | Spatial |
| 13 | Martin and Norris 2007 ^{MPB,A} | BC | Peaked 2003 | M | 1995–2004 | ≥10 ⁷ | Spatial |
| 14 | Martin et al. 2006 ^{PR,MPB,A} | BC | Peaked 2003 | M | 1995–2005 | ≥10 ⁷ | Temporal |
| 15 | Mosher 2011 ^{MPB,A,M} | MT | 2006–2010; peaked 2008 | MP | 2003–2006, 2009–2010 | 362,000 | Temporal |
| 16 | Munro et al. 2008 ^{MPB,S,M} | BC, MT | 1976–1984 | ML | 1978–2008 | 20,600 | Spatial |
| 17 | Norris and Martin 2008 ^{PR,MPB,A} | BC | Peaked 2003 | M | 1995–2005 | ≥10 ⁷ | Spatial |
| 18 | Norris and Martin 2010 ^{PR,MPB,A} | BC | Peaked 2003 | M | 1997–2006 | ≥10 ⁷ | Temporal and spatial |
| 19 | Norris & Martin 2013 ^{PR,MPB,A} | BC | Peaked 2003 | M | 1997–2006 | ≥10 ⁷ | Temporal and spatial |
| 20 | V.A. Saab et al., unpubl. data, 2012 ^{MPB,N,A} | MT | 2006–2010; peaked 2008 | MP | 2003–2006, 2009–2011 | 362,000 | Temporal |
| 21 | Seip and Jones 2009 ^{MPB,S,M} | BC | 2006 | L | 2006–2009 | Not reported | Spatial |
| 22 | Stone 1995 ^{MPB,A,M} | UT | 1980–1987 | L | 1988–1992 | Not reported | Spatial |
| 23 | Sullivan et al. 2010 ^{PR,MPB,S,M} | BC | 1970s | M | 2005–2008 | Not reported | Temporal and spatial |

State/province locations reported: South Dakota (SD), Oregon (OR), British Columbia (BC), Montana (MT), and Utah (UT). Forest types (Veg) were described as ponderosa or lodgepole pine-dominant (P, L), mixed conifer with ponderosa or lodgepole pine-dominant (MP, ML), or mixed conifer with no dominant species indicated (M). Study designs compared wildlife response metrics before versus after the outbreak (temporal), across sites that varied in degree or intensity of response (spatial), or both.

^N Unpublished data are referenced as “novel studies” in the text.

^{MPB} Studies that examined wildlife relationships with MPB outbreak.

^S Studies that examined wildlife relationships with postoutbreak salvage logging.

^{PR} Studies published in peer-reviewed sources.

^A Studies that report avian relationships.

^M Studies that report mammalian relationships.

For groups reliant on live trees for food, our review included data on 16 foliage insectivores and 5 pine seed consumers. Foliage insectivore relationships were variable. Nine foliage insectivore species displayed negative relationships, whereas 11 foliage insectivore species showed demographic increases in relation to MPB outbreaks. Only two foliage-insectivorous species (Cassin’s vireo [*Vireo cassinii*] and magnolia warbler [*Setophaga magnolia*]) never exhibited either positive or negative relationships, but these species were the least studied (represented in two and one studies, respectively). The five species of pine seed consumers (white-headed woodpecker, Clark’s nutcracker, pine grosbeak, and two crossbills) did not reveal any changes in relation to MPB outbreaks, although this group was not well studied (represented in one to two studies each).

Our review included data on 14 shrub-nesting, 13 ground-nesting, and 7 ground or near-ground insectivore species. Most studies were conducted 2–6 years after peak tree mortality, probably not long enough for increased growth in the understory vegetation (cf. Stone and Wolfe 1996). Three studies, however, reported changes in avian population metrics 15 years after peak tree mortality, allowing time for snags to fall followed by increased light and shrub growth in the understory (cf. Page and Jenkins 2007). As a group, shrub-nesting species tended to relate positively with MPB outbreaks. Only five shrub-nesting species exhibited no apparent change in relation to MPB outbreaks.

Responses by ground insectivores and ground-nesting species were more mixed. Three ground insectivores demonstrated positive

associations, but two exhibited negative relationships, and one (winter wren [*T. hiemalis*]) showed an apparent mixed relationship within one study (Chan-McLeod et al. 2008). Three ground-nesting species tended to relate positively with MPB outbreaks, whereas five species related negatively. Dark-eyed junco (*Junco hyemalis*) tended to show positive relationships, whereas northern waterthrush (*Parkesia noveboracensis*) and veery (*Catharus fuscescens*) (both nest and forage on the ground) did not reveal any response to a MPB epidemic, although they were only represented in one study.

Twenty-five avian species were studied in beetle-killed forests characterized as either lodgepole pine- or ponderosa pine-dominant, disregarding forests described as “mixed conifer” with no particular dominant tree species reported (Tables 2 and 3). Five species (downy woodpecker, American robin, mountain bluebird, chipping sparrow, and Cassin’s finch) consistently showed positive relationships with MPB outbreaks in both forest types. Two species, Swainson’s thrush (*Catharus ustulatus*) and warbling vireo, exhibited negative relationships in lodgepole pine while exhibiting positive relationships in ponderosa pine forests affected by MPB outbreaks. Eight species showed no relationship with MPB outbreaks in either forest type. Of 10 cavity-nesting species, 3 and 4 species demonstrated positive relationships in ponderosa and lodgepole pine forests (2 species in both), respectively. Two species (red-breasted nuthatch and mountain chickadee) tended to relate negatively, but only in lodgepole pine forests affected by MPB outbreaks. Five cavity-nesting species (black-backed woodpecker, northern flicker,

Table 3. Avian relationships with MPB outbreaks reported in reviewed studies.

| Species (taxonomic name; assemblage: foraging, nest layer, nest type) | Ref. | No. sites | <i>n</i> | Response type | Response |
|---|------|-----------------|---------------------------|--|--------------------|
| Bufflehead (<i>Bucephala albeola</i> ; OM, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Sharp-shinned hawk (<i>Accipiter striatus</i> ; CA, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Cooper's hawk (<i>Accipiter cooperii</i> ; CA, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Northern goshawk (<i>Accipiter gentilis</i> ; CA, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Red-tailed hawk (<i>Buteo jamaicensis</i> ; CA, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| American kestrel (<i>Falco sparverius</i> ; CA, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Dusky grouse (<i>Dendragapus obscurus</i> ; OM, GR, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Ruffed grouse (<i>Bonasa umbellus</i> ; OM, GR, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Mourning dove (<i>Zenaidura macroura</i> ; OM, SH, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Barred owl (<i>Strix varia</i> ; CA, CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Great gray owl (<i>Strix nebulosa</i> ; CA, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Great-horned owl (<i>Bubo virginianus</i> ; CA, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Northern saw-whet owl (<i>Aegolius acadicus</i> ; CA, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Common nighthawk (<i>Chordeiles minor</i> ; AI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Rufous hummingbird (<i>Selasphorus rufus</i> ; NE, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| American three-toed woodpecker (<i>Picoides dorsalis</i> ; BD, CA, Cp) | 3 | 4 ^{C1} | 48 points | Relative abundance ^S | None ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^S | + |
| | 10 | 20 | 317 nests | No. eggs/nestlings per nest ^T | None |
| | 14 | 27 | Not recorded | Nest density ^T | + ^{NP} |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| | 20 | 4 | 33 nests | Nest density ^T | + |
| | 20 | 4 | 33 nests | Nest survival ^T | NS |
| | 20 | 4 | 33 nests | Nest survival ^S | NS |
| Black-backed woodpecker (<i>Picoides arcticus</i> ; BD, CA, Cp) | 1 | ≥52 | 43 nests | Nest site selection ^S | NS ^{NP} |
| | 2 | ≥52 | 42 nests | Relative abundance ^{S,W} | NS ^{NP} |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^T | + |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^T | NS |
| | 9 | 23 | 242 point-years | Relative abundance ^S | NS |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^S | + |
| | 10 | 20 | 91 nests | No. eggs/nestlings per nest ^T | NS |
| Downy woodpecker (<i>Picoides pubescens</i> ; BD, CA, Cp) | 14 | 27 | Not recorded | Nest density ^T | + ^{NP} |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| | 20 | 4 | 31 nests | Nest density ^T | NS |
| | 20 | 4 | 31 nests | Nest survival ^T | NS |
| | 22 | 40 | 160 points | Relative density ^S | + |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | + ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^S | + |
| | 10 | 20 | 68 nests | No. eggs/nestlings per nest ^T | NS |
| Hairy woodpecker (<i>Picoides villosus</i> ; BD, CA, Cp) | 14 | 27 | Not recorded | Nest density ^T | + ^{NP} |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| | 20 | 4 | 43 nests | Nest density ^T | + |
| | 20 | 4 | 43 nests | Nest survival ^T | NS |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^S | NS |
| | 10 | 20 | 317 nests | No. eggs/nestlings per nest ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Northern flicker (<i>Colaptes auratus</i> ; OM, CA, Cp) | 20 | 4 | 27 nests | Nest density ^T | NS |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^S | NS |
| | 10 | 20 | 317 nests | No. eggs/nestlings per nest ^T | NS |
| 15 | 4 | 80 points | Occupancy ^T | NS | |
| 20 | 4 | 27 nests | Nest density ^T | NS | |

(continued)

Table 3. (Continued.)

| Species (taxonomic name; assemblage: foraging, nest layer, nest type) | Ref. | No. sites | <i>n</i> | Response type | Response | |
|---|---|-----------------|--------------------|---|---|------------------|
| Northern flicker (<i>Colaptes auratus</i> ; OM, CA, Cp) | 20 | 4 | 27 nests | Nest survival ^T | NS | |
| | 22 | 40 | 160 points | Relative density ^S | NS | |
| | Pileated woodpecker (<i>Dryocopus pileatus</i> ; OM, CA, Cp) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | | 4 | 7 ^{IS} | Not recorded for density; 11 pairs for reproductive success | density and reproductive success ^T | NS ^{C2} |
| | | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | | 9 | 23 | 242 point-years | Relative abundance ^S | + |
| | | 14 | 27 | Not recorded | Nest density ^T | NS ^{NP} |
| | | 15 | 4 | 80 points | Occupancy ^T | NS |
| | Red-naped sapsucker (<i>Sphyrapicus nuchalis</i> ; OM, CA, Cp) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| 9 | | 23 | 242 point-years | Relative abundance ^T | NS | |
| 9 | | 23 | 242 point-years | Relative abundance ^S | NS | |
| 10 | | 20 | 284 nests | No. eggs/nestlings per nest ^T | NS | |
| 15 | | 4 | 80 points | Occupancy ^T | NS | |
| 20 | | 4 | 95 nests | Nest density ^T | NS | |
| 20 | | 4 | 95 nests | Nest survival ^T | NS | |
| White-headed woodpecker (<i>Picoides albolarvatus</i> ; OM, CA, Cp) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} | |
| Alder flycatcher (<i>Empidonax alnorum</i> ; AI, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| Dusky flycatcher (<i>Empidonax oberholseri</i> ; AI, SH, O) | 15 | 4 | 80 points | Occupancy ^T | + | |
| Hammond's flycatcher (<i>Empidonax hammondi</i> ; AI, CA, O) | 15 | 4 | 80 points | Occupancy ^T | + | |
| Least flycatcher (<i>Empidonax minimus</i> ; AI, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + | |
| Olive-sided flycatcher (<i>Contopus cooperi</i> ; AI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – | |
| | 22 | 40 | 160 points | Relative density ^S | + | |
| Pacific-slope flycatcher (<i>Empidonax difficilis</i> ; AI, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| Western wood pewee (<i>Contopus sordidulus</i> ; AI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – | |
| Willow flycatcher (<i>Empidonax traillii</i> ; AI, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + | |
| Tree swallow (<i>Tachycineta bicolor</i> ; AI, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| | 15 | 4 | 80 points | Occupancy ^T | NS | |
| Violet-green swallow (<i>Tachycineta thalassina</i> ; AI, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| American crow (<i>Corvus brachyrhynchos</i> ; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| Black-billed magpie (<i>Pica hudsonia</i> ; OM, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} | |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| Clark's nutcracker (<i>Nucifraga columbiana</i> ; PSC, CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS | |
| Common raven (<i>Corvus corax</i> ; OM, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} | |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – | |
| | 15 | 4 | 80 points | Occupancy ^T | + | |
| | Gray jay (<i>Perisoreus canadensis</i> ; OM, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| | | 6 | 21 | 116 points | Relative abundance ^S | + ^{NP} |
| Steller's jay (<i>Cyanocitta stelleri</i> ; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| | 15 | 4 | 80 points | Occupancy ^T | NS | |
| | 22 | 40 | 160 points | Relative density ^S | NS | |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} | |
| | 15 | 4 | 80 points | Occupancy ^T | NS | |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS | |
| Black-capped chickadee (<i>Poecile atricapillus</i> ; FI, CA, Cs) | 14 | 27 | Not recorded | Nest density ^T | NS ^{NP} | |
| | 15 | 4 | 80 points | Occupancy ^T | – | |
| Boreal chickadee (<i>Poecile hudsonicus</i> ; FI, CA, C) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + | |
| Mountain chickadee (<i>Poecile gambeli</i> ; FI, CA, Cs) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | – ^{NP} | |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + | |
| | 13 | 16 | 4,458 point-visits | population growth ^S | + ^{C7} | |
| | 14 | 27 | Not recorded | Nest density ^T | + ^{NP} | |
| | 15 | 4 | 80 points | Occupancy ^T | NS | |
| | 19 | 27 | 425 points | Relative density ^B | + ^{C6} | |
| Brown creeper (<i>Certhia americana</i> ; BG, CA, Cs) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} | |
| | 6 | 21 | 116 points | Relative abundance ^S | mixed ^{NP,C3} | |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + | |
| | 15 | 4 | 80 points | Occupancy ^T | NS | |

(continued)

Table 3. (Continued.)

| Species (taxonomic name; assemblage: foraging, nest layer, nest type) | Ref. | No. sites | <i>n</i> | Response type | Response |
|---|------|-----------------|--------------------------------|-----------------------------------|------------------------|
| Red-breasted nuthatch (<i>Sitta canadensis</i> ; BG, CA, Cp) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | – ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 14 | 27 | Not recorded | Nest density ^T | Mixed ^{NP,C4} |
| | 15 | 4 | 80 | Occupancy ^T | NS |
| | 17 | 27 | 231 nests; 1,136 random points | Nest site selection ^S | + |
| | 18 | 27 | 425 points | Relative density ^B | + ^{C6} |
| White-breasted nuthatch (<i>Sitta carolinensis</i> ; BG, CA, Cs) | 22 | 40 | 160 points | Relative density ^S | + |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| House wren (<i>Troglodytes aedon</i> ; GI, CA, Cs) | 15 | 4 | 80 points | Occupancy ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Winter wren (<i>Troglodytes hiemalis</i> ; GI, CA, Cs) | 6 | 21 | 116 points | Relative abundance ^S | mixed ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Golden-crowned kinglet (<i>Regulus satrapa</i> ; FI, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | – ^{NP} |
| | 6 | 21 | 116 points | Relative abundance ^S | + ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| Ruby-crowned kinglet (<i>Regulus calendula</i> ; FI, CA, O) | 6 | 21 | 116 points | Relative abundance ^S | NS ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 14 | 27 | Not recorded | Nest density ^T | NS ^{NP} |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| American robin (<i>Turdus migratorius</i> ; GI, CA, O) | 6 | 21 | 116 points | Relative abundance ^S | + ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Hermit thrush (<i>Catharus guttatus</i> ; GI, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Mountain bluebird (<i>Sialia currucoides</i> ; AI, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| | 22 | 40 | 160 points | Relative density ^S | + |
| Swainson's thrush (<i>Catharus ustulatus</i> ; FI, SH, O) | 6 | 21 | 116 points | Relative abundance ^S | – ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Townsend's solitaire (<i>Myadestes townsendi</i> ; AI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Varied thrush (<i>Ixoreus naevius</i> ; GI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Veery (<i>Catharus fuscescens</i> ; GI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| European starling (<i>Sturnus vulgaris</i> ; GI, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Cedar waxwing (<i>Bombycilla cedrorum</i> ; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Cassin's vireo (<i>Vireo cassinii</i> ; FI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Warbling vireo (<i>Vireo gilvus</i> ; FI, CA, O) | 6 | 21 | 116 points | Relative abundance ^S | – ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Blackpoll warbler (<i>Setophaga striata</i> ; BG, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| MacGillivray's warbler (<i>Geothlypis tolmiei</i> ; FI, SH, O) | 15 | 4 | 80 points | Occupancy ^T | + |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Northern waterthrush (<i>Parkesia noveboracensis</i> ; GI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| Orange-crowned warbler (<i>Oreothlypis celata</i> ; FI, GR, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| Townsend's warbler (<i>Setophaga townsendi</i> ; FI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| Wilson's warbler (<i>Cardellina pusilla</i> ; FI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| Yellow warbler (<i>Setophaga petechia</i> ; FI, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 6 | 21 | 116 points | Relative abundance ^S | NS ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| Yellow-rumped warbler (<i>Setophaga coronata</i> ; FI, CA, O) | 22 | 40 | 160 points | Relative density ^S | NS |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Chipping sparrow (<i>Spizella passerina</i> ; OM, SH, O) | 22 | 40 | 160 points | Relative density ^S | + |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| 22 | 40 | 160 points | Relative density ^S | + | |

(continued)

Table 3. (Continued.)

| Species (taxonomic name; assemblage: foraging, nest layer, nest type) | Ref. | No. sites | <i>n</i> | Response type | Response |
|---|------|-----------------|--------------------|-----------------------------------|-----------------|
| Dark-eyed junco (<i>Junco hyemalis</i> ; OM, GR, O) | 6 | 21 | 116 points | Relative abundance ^S | – ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| | 22 | 40 | 160 points | Relative density ^S | + |
| Lincoln's sparrow (<i>Melospiza lincolni</i> ; OM, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Savannah sparrow (<i>Passerculus sandwichensis</i> ; OM, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| Song sparrow (<i>Melospiza melodia</i> ; GI, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Vesper sparrow (<i>Poocetes gramineus</i> ; OM, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| White-crowned sparrow (<i>Zonotrichia leucophrys</i> ; OM, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Black-headed grosbeak (<i>Pheucticus melanocephalus</i> ; OM, CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Lazuli bunting (<i>Passerina amoena</i> ; OM, SH, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Brewer's blackbird (<i>Euphagus cyanocephalus</i> ; OM, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| Brown-headed cowbird (<i>Molothrus ater</i> ; OM, –, P) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Rusty blackbird (<i>Euphagus carolinus</i> ; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| Western tanager (<i>Piranga ludoviciana</i> ; FI, CA, O) | 6 | 21 | 116 points | Relative abundance ^S | – ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| | 22 | 40 | 160 points | Relative density ^S | + |
| Pine grosbeak (<i>Pinicola enucleator</i> ; PSC, CA, O) | 22 | 40 | 160 points | Relative density ^S | NS |
| Cassin's finch (<i>Haemorhous cassinii</i> ; OM, CA, O) | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | + ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Pine siskin (<i>Spinus pinus</i> ; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Red crossbill (<i>Loxia curvirostris</i> ; PSC, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | NS |
| White-winged crossbill (<i>Loxia leucoptera</i> ; PSC, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Evening grosbeak (<i>Coccothraustes vespertinus</i> ; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + ^{C5} |

Species belonged to one of nine foraging assemblages: aerial insectivores (AI), bark-drilling insectivores (BD), bark-gleaning insectivores (BG), foliage insectivores (FI), ground insectivores (GI), carnivores (CA), nectarivores (NE), pine seed consumers (PSC), or omnivores (OM); one of three nest-layer assemblages: ground layer (GR), shrub layer (SH), or canopy layer (CA); and one of two nest types: cavity (Cp = primary [excavator] and Cs = secondary [nonexcavator]) or open cup (O). Reference numbers (Ref.) indicate the study number (Table 2) that provided the information. Relationships are classified as positive (+), negative (–), mixed, or nonSignificant (NS).

^S Indicates studies with spatial comparisons.

^T Indicates studies with temporal comparisons.

^B Indicates studies with both spatial and temporal comparisons.

^W Study conducted in winter.

^{NP} Indicates studies with no statistical analyses or estimate of precision for parameter describing relationship.

^{C1} This study lacks replication. Four distinct treatments associated with different levels of MPB attack severity are identified, but only one site was surveyed within each treatment.

^{C2} Responses to MPB were not the focus of the study. Reports no apparent change despite multiple insect outbreaks across study period.

^{C3} Reports a negative relationship with % basal area of pines infested but a positive relationship with % stems per ha infested.

^{C4} Study reports a positive relationship in one area but a negative relationship in another.

^{C5} Reportedly a probable response to concurrent spruce budworm outbreak.

^{C6} Mechanism for relationship provided: increased availability of cavities provided by downy woodpeckers.

^{C7} Population growth was estimated based on time-series analysis. Growth was less density-dependent in areas with a greater proportion of lodgepole pines with MPB.

pileated woodpecker, brown creeper, and white-breasted nuthatch) exhibited only nonsignificant or mixed relationships in ponderosa pine- or lodgepole pine-dominant forests.

Four studies that examined species-specific responses also reported changes in total bird abundance and avian species richness in relation to MPB outbreaks (Table 3). Two reported nonsignificant changes in both metrics (Drever and Martin 2007, Chan-McLeod et al. 2008) and one reported a parabolic relation in both metrics, whereby both total abundance and richness peaked at intermediate

outbreak intensities (Stone 1995). Bull (1983), who provided no statistical analysis, reported lower overall numbers but greater species richness in outbreak-affected stands.

Woodpecker Nest Survival and Densities in Western Montana

Nest survival patterns for woodpeckers in our western Montana study provided some evidence for our predictions, although low precision associated with nest survival estimates limited our inferences (Figure 1A). Increased nest survival rates after the outbreak

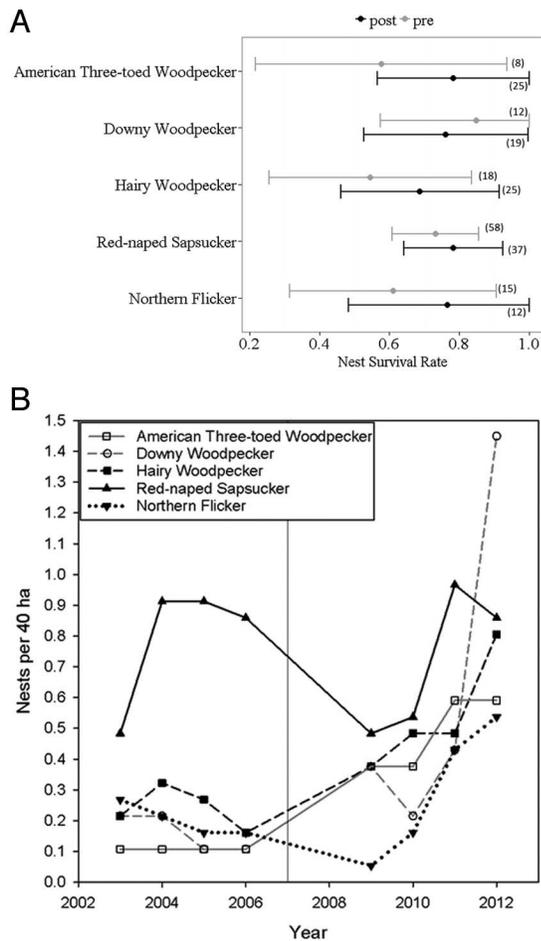


Figure 1. A. Period nest survival rates (mean \pm 95% CI) for woodpeckers before (2003–2006) and after (2009–2011) a MPB outbreak in western Montana dry mixed conifer forests. Numbers in parentheses are nest sample sizes. B. Relative nest densities for woodpeckers by year surveyed in a MPB outbreak in western Montana dry mixed conifer forests. The vertical line indicates the start of the MPB outbreak.

were consistent with our predictions for two beetle foraging specialists, American three-toed and hairy woodpeckers. The magnitude of this increase was greater than that for other woodpecker species. As expected, we observed less change in nest survival for red-naped sapsucker than for beetle foraging specialists. Northern flicker nest survival rates, however, increased by an amount similar to that of hairy woodpeckers.

Nest densities of bark-drilling specialists (American three-toed, hairy, and downy woodpeckers) increased with time since the outbreak as predicted (Figure 1B). In contrast, during 2009–2010 (2 years after the 2008 peak in beetle-caused tree mortality), red-naped sapsucker, and Northern flicker nest densities were lower than pre-outbreak levels. By 2011, however, their nesting densities exceeded those observed during the preoutbreak period.

Nonavian Relationships with MPB Outbreaks

Published studies describing responses of nonavian vertebrates to MPB outbreaks were rare ($n = 5$) (Table 4), and none were peer-reviewed. We supplemented these with two novel studies on small mammals in southern Wyoming. We found no literature describing

empirical studies of reptile or amphibian responses to MPB outbreaks; thus, our nonavian results are confined to studies of 12 mammalian species that included four ungulates and a variety of small mammals (Table 4). Relative abundance was the dominant response variable reported; authors also described occupancy and habitat use as response types. Only two studies used spatial replication. Sampling units were varied and included radiocollared animals, transects, circular plots, and points or point-visits. Only one study of northern caribou (*Rangifer tarandus*) involved winter observations. Most studies reported spatial comparisons of changes in population parameters in relation to MPB outbreaks, typically among sites with different levels of mortality or degree of infestation by MPBs. Two studies of red squirrels (Drever and Martin 2007, Mosher 2011) evaluated temporal trends in red squirrel numbers before and during an epidemic. No studies described both spatial and temporal responses of mammals to MPB outbreaks. Studies of mammalian responses to MPB outbreaks were conducted almost exclusively in lodgepole pine forests.

The effects of MPB outbreaks on mammals were variable. Five species exhibited positive associations, including three of four ungulates; four species showed mixed relationships, including snowshoe hare (*Lepus americanus*), two chipmunk species, and southern red-backed vole. Only one species, red squirrel, exhibited a negative association with MPB outbreaks. Nonsignificant relationships with recent MPB outbreaks were reported for three species, including northern caribou, deer mouse (*Peromyscus maniculatus*), and red squirrel.

Most mammalian species' relationships with MPB outbreaks that we report were described by Stone (1995), who examined mammalian community responses to lodgepole pine mortality that ranged from 14 to 95% for all size classes during an epidemic in northern Utah. Results are reported as species abundance and diversity responses as a function of increasing tree mortality. This study is the only empirical information we identified that reported relationships with MPB outbreaks for elk, mule deer (*Odocoileus hemionus*), moose (*Alces alces*), snowshoe hare, northern flying squirrel (*Glaucomys sabrinus*), golden-mantled ground squirrel (*Callospermophilus lateralis*), southern red-backed vole, chipmunks (*Neotamias minimus* or *Neotamias umbrinus*), and deer mouse (*Peromyscus maniculatus*). Mammalian community diversity was higher in beetle-killed stands than in unaffected stands.

Red Squirrel Occurrence in Southern Wyoming

We recorded 361 detections of red squirrels in 2011 ($n = 105$) and 2012 ($n = 256$). Live stand basal area ranged from 0 to 27 m^2/ha in both watersheds. Our logistic regression model fit the data adequately ($z = 0.97$, $P = 0.33$) and described a significant relationship between squirrel occurrence probability (i.e., detection and occurrence) and the total amount of live basal area ($\beta = 0.07$, $z = 2.74$, $P < 0.01$). The model controlled for significant interannual variation in occurrence probability ($\beta = 0.81$, $z = 3.66$, $P < 0.001$) and weak variation between watersheds ($\beta = 0.04$, $z = 0.20$, $P = 0.85$). The probability of observing a red squirrel was higher in 2012 and was positively related to live basal area across sampling points in both years (Figure 2). Controlling for year, each 1- m^2 increase in live basal area per ha increased the odds of observing a squirrel by 1.07 times (95% CI, 1.02–1.13). Over the observed range of variation of live basal area at sampling points (27 m^2/ha), this corresponds to a change in the odds of encountering a squirrel by 29-fold, which we believe is biologically significant. Controlling for the

Table 4. Mammalian relationships with MPB outbreaks as reported in articles reviewed.

| Species (taxonomic name) | Ref. | No. sites | <i>N</i> | Response type | Response |
|---|------|-----------|-------------------------------------|--------------------------------------|--------------------------|
| Snowshoe hare (<i>Lepus americanus</i>) | 22 | 40 | 50–10 m ² circular plots | Relative abundance ^S | Mixed ^{C1} |
| Chipmunk (<i>Neotamias minimus</i> and <i>Neotamias umbrinus</i>) | 22 | 40 | 8 transects | Relative abundance ^S | Mixed ^{C2} |
| Golden-mantled ground squirrel (<i>Callospermophilus lateralis</i>) | 22 | 40 | 8 transects | Relative abundance ^S | + ^{C3} |
| Red squirrel (<i>Tamiasciurus hudsonicus</i>) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | – |
| | 11 | 2 | 360 point-year samples; 180 points | Relative abundance ^S | – ^{C4} |
| | 15 | 4 | 76 points | Occupancy ^T | NS ^{C5} |
| | 22 | 40 | 8 transects | Relative abundance ^S | – ^{C6} |
| Northern flying squirrel (<i>Glaucomys sabrinus</i>) | 22 | 40 | 8 transects | Relative abundance ^S | + ^{C3} |
| Deer mouse (<i>Peromyscus maniculatus</i>) | 22 | 40 | 8 transects | Relative abundance ^S | NS |
| Southern red-backed vole (<i>Clethrionomys gapperi</i>) | 22 | 40 | 8 transects | Relative abundance ^S | Mixed ^{C2} |
| | 5 | 38 | 38 patches | Abundance ^S | NS |
| Elk (<i>Cervus canadensis</i>) | 22 | 40 | 50–10 m ² circular plots | Relative abundance ^S | + ^{C3} |
| Mule deer (<i>Odocoileus hemionus</i>) | 22 | 40 | 50–10 m ² circular plots | Relative abundance ^S | + ^{C3} |
| Moose (<i>Alces alces</i>) | 22 | 40 | 50–10 m ² circular plots | Relative abundance ^S | + ^{C3} |
| Northern caribou (<i>Rangifer tarandus</i>) | 7 | 1 | 38 caribou | No. animal locations ^{S, W} | NS ^{NP, C7, C8} |

Reference numbers (Ref.) indicate the study number (Table 2) that provided the information. Responses are classified as positive (+), negative (–), mixed, or nonsignificant (NS).

^S Indicates studies with spatial comparisons.

^T Indicates studies with temporal comparisons.

^W Indicates study conducted in winter.

^{NP} Indicates studies with no statistical analyses or estimate of precision for parameter describing relationship.

^{C1} No effect in 1990, but in 1991 pellet groups were most abundant in plots with moderate tree mortality.

^{C2} Most abundant in plots with moderate tree mortality.

^{C3} More abundant in stands with moderate to high tree mortality than stands with low mortality.

^{C4} Positive relationship with live basal area.

^{C5} Detection probability decreased from pre-epidemic to epidemic time period.

^{C6} Less abundant in plots with higher tree mortality.

^{C7} No observed difference in habitat use (both site and stand scales) or seasonal movements between the pre-MPB and grey attack phases of MPB outbreak.

^{C8} No replication was used in this study; radiolocations from individual animals were pooled to evaluate habitat use across seasonal ranges within a single study area.

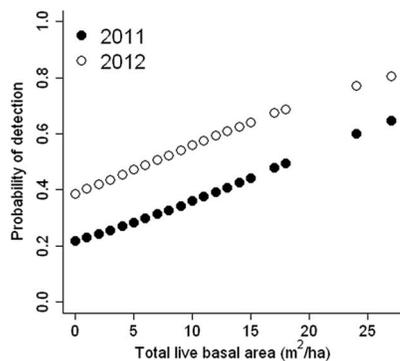


Figure 2. Predicted probabilities of a red squirrel detection in relation to increasing levels of live stand basal area. Data were collected (2011–2012) at two watersheds in the Sierra Madre Range, Southcentral Wyoming.

amount of live basal area, the odds of observing a squirrel in 2012 were 2.25 times (95% CI, 1.46–3.50) the odds of observing a squirrel in 2011. Watershed had no significant effect.

Our results were consistent with previous studies that also reported negative effects of beetle-induced tree mortality on red squirrels (Matsuoka et al. 2001, Drever and Martin 2007). Zugmeyer and Koprowski (2009a, 2009b) found habitat use by the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) was not affected by forest changes associated with bark beetle activity until tree mortality exceeded 64%. Average percent mortality for all tree species and size classes at our study site was only 24%. Differential responses to tree mortality among these studies may be influenced by differences in the age structure of the remaining live

trees. Red squirrels may occur more frequently in areas with more live trees because these areas provide more food resources (i.e., greater seed production) and higher canopy cover, which may facilitate evasion of raptor predators (Zugmeyer and Koprowski 2009b).

Southern Red-Backed Vole Density in Southern Wyoming

Percent dead lodgepole in our patches ranged from 0 to 30% (5.8 ± 1.3) and percent dead spruce ranged from 0 to 60% (15.4 ± 2.7). Neither percent lodgepole ($t = -0.93$, $P = 0.36$, $\beta = -0.10 \pm 0.10$) nor percent spruce ($t = -0.64$, $P = 0.53$, $\beta = -0.03 \pm 0.05$) mortality was significantly related to red-backed vole abundance.

Wildlife Responses to Postoutbreak Salvage Logging

Three studies (all peer-reviewed) examined responses by 27 avian species to salvage logging after MPB outbreaks (Table 5). Two studies were conducted in the same British Columbia study area, characterized by mixed deciduous/coniferous forests, where the deciduous component was dominated by trembling aspen and the dry coniferous forest was composed of lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), and spruce (*Picea* spp.) (Drever and Martin 2010, Edworthy et al. 2011). These two studies reported variable harvest treatments, i.e., “partial harvest” described as 15–30% tree removal and clear cuts characterized by 50–90% removal of trees >12.5 cm dbh (Drever and Martin 2010, Edworthy et al. 2011). Most live aspen and Douglas-fir trees of various diameter classes were retained, either as reserves or spread throughout the harvest units. Live trees serve as important wildlife habitat, a key point when considering the effects of postbeetle salvage logging. In contrast,

Table 5. Avian and mammalian relationships with salvage logging after MPB outbreaks reported in reviewed articles.

| Class | Species (taxonomic name) | Ref. | No. sites | <i>n</i> | Response type | Response | |
|---|---|--|---------------------|-----------------------|---|------------------------|------------------|
| Aves | American three-toed woodpecker (<i>Picoides dorsalis</i>) | 9 | 23 | 242 point-years | Count ^B | NS | |
| | | 10 | 20 | 317 nests | No. eggs or nestlings per nest ^B | NS | |
| | Black-backed woodpecker (<i>Picoides arcticus</i>) | 9 | 23 | 242 point-years | Count ^B | NS | |
| | | 12 | 24 | 193 points | Abundance ^S | NS ^{C1,C2} | |
| | Downy woodpecker (<i>Picoides pubescens</i>) | 9 | 23 | 242 point-years | Count ^B | + | |
| | | 10 | 20 | 91 nests | No. eggs or nestlings per nest ^B | NS | |
| | Hairy woodpecker (<i>Picoides villosus</i>) | 9 | 23 | 242 point-years | Count ^B | + ^{C3} | |
| | | 10 | 20 | 68 nests | No. eggs or nestlings per nest ^B | NS | |
| | | 12 | 24 | 203 points | Abundance ^S | NS ^{C1,C2} | |
| | Northern flicker (<i>Colaptes auratus</i>) | 9 | 23 | 242 point-years | Count ^B | + ^{C4} | |
| | | 10 | 20 | 317 nests | No. eggs or nestlings per nest ^B | NS | |
| | Pileated woodpecker (<i>Dryocopus pileatus</i>) | 9 | 23 | 242 point-years | Count ^B | + ^{C4} | |
| | | 10 | 20 | 29 nests | No. eggs or nestlings per nest ^B | NS | |
| | Red-naped sapsucker (<i>Sphyrapicus nuchalis</i>) | 9 | 23 | 242 point-years | Count ^B | + | |
| | | 10 | 20 | 284 nests | No. eggs or nestlings per nest ^B | NS | |
| | Dusky flycatcher (<i>Empidonax oberholseri</i>) | 12 | 24 | 199 points | Abundance ^S | NS ^{C1,C2} | |
| | Gray flycatcher (<i>Empidonax wrightii</i>) | 12 | 24 | 200 points | Abundance ^S | NS ^{C1,C2,C3} | |
| | Gray jay (<i>Perisoreus canadensis</i>) | 12 | 24 | 201 points | Abundance ^S | NS ^{C1,C2} | |
| | Mountain chickadee (<i>Poecile gambeli</i>) | 12 | 24 | 206 points | Abundance ^S | NS ^{C1,C2} | |
| | Brown creeper (<i>Certhia americana</i>) | 12 | 24 | 194 points | Abundance ^S | NS ^{C1,C2} | |
| | Red-breasted nuthatch (<i>Sitta canadensis</i>) | 12 | 24 | 209 points | Abundance ^S | NS ^{C1,C2} | |
| | White-breasted nuthatch (<i>Sitta carolinensis</i>) | 12 | 24 | 212 points | Abundance ^S | NS ^{C1,C2} | |
| | American robin (<i>Turdus migratorius</i>) | 12 | 24 | 192 points | Abundance ^S | NS ^{C1,C2} | |
| | Hermit thrush (<i>Catharus guttatus</i>) | 12 | 24 | 204 points | Abundance ^S | NS ^{C1,C2} | |
| | Mountain bluebird (<i>Sialia currucoides</i>) | 12 | 24 | 205 points | Abundance ^S | NS ^{C1,C2} | |
| | Townsend's solitaire (<i>Myadestes townsendi</i>) | 12 | 24 | 210 points | Abundance ^S | NS ^{C1,C2} | |
| | Yellow-rumped warbler (<i>Setophaga coronata</i>) | 12 | 24 | 213 points | Abundance ^S | NS ^{C1,C2} | |
| | Green-tailed towhee (<i>Pipilo chlorurus</i>) | 12 | 24 | 202 points | Abundance ^S | NS ^{C1,C2} | |
| | Chipping sparrow (<i>Spizella passerina</i>) | 12 | 24 | 197 points | Abundance ^S | NS ^{C1,C2} | |
| | Dark-eyed junco (<i>Junco hyemalis</i>) | 12 | 24 | 198 points | Abundance ^S | + ^{C1,C2} | |
| | Brown-headed cowbird (<i>Molothrus ater</i>) | 12 | 24 | 195 points | Abundance ^S | NS ^{C1,C2} | |
| | Western tanager (<i>Piranga ludoviciana</i>) | 12 | 24 | 211 points | Abundance ^S | NS ^{C1,C2} | |
| | Cassin's finch (<i>Haemorhous cassinii</i>) | 12 | 24 | 196 points | Abundance ^S | + ^{C1,C2} | |
| | Pine siskin (<i>Spinus pinus</i>) | 12 | 24 | 207 points | Abundance ^S | NS ^{C1,C2} | |
| | Red crossbill (<i>Loxia curvirostra</i>) | 12 | 24 | 208 points | Abundance ^S | NS ^{C1,C2} | |
| | Mammalia | Common shrew (<i>Sorex araneus</i>) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | | Montane shrew (<i>Sorex monticolus</i>) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | | Northwestern chipmunk (<i>Neotamias amoenus</i>) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | | Red squirrel (<i>Tamiasciurus hudsonicus</i>) | 23 | 12 | 1,200 trapping stations | Abundance ^B | NS ^{C5} |
| | | Northern flying squirrel (<i>Glaucomys sabrinus</i>) | 23 | 12 | 1,200 trapping stations | Abundance ^B | NS |
| | | Deer mouse (<i>Peromyscus maniculatus</i>) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| Southern red-backed vole (<i>Clethrionomys gapperi</i>) | | 23 | 12 | 588 trapping stations | Abundance ^B | - ^{C6} | |
| Heather vole (<i>Phenacomys intermedius</i>) | | 23 | 12 | 588 trapping stations | Abundance ^B | + ^{C7} | |
| Long-tailed vole (<i>Microtus longicaudus</i>) | | 23 | 12 | 588 trapping stations | Abundance ^B | NS | |
| Meadow vole (<i>Microtus pennsylvanicus</i>) | | 23 | 12 | 588 trapping stations | Abundance ^B | NS | |
| Grizzly bear (<i>Ursus arctos</i>) | | 16 | 2 ^{C8} | 396 hair snare sites | Occupancy ^S | + ^{C9} | |
| | | 16 | 2 ^{C8} | 396 hair snare sites | Abundance ^S | NS ^{C10} | |
| | | 16 | 2 ^{C8} | 33 mortalities | Mortality risk ^S | - ^{C11} | |
| Caribou (<i>Rangifer tarandus</i>) | | 21 | 1 ^{C12,IS} | 21 radioed animals | No. animal locations ^{S,W} | - ^{C13,NP} | |

Reference numbers (Ref.) indicate the study number (Table 2) that provided the information. Responses are classified as positive (+), negative (-), mixed, or nonsignificant (NS).

^{IS} Indicates study with inconsistent sampling.

^S Indicates studies with spatial comparisons.

^T Indicates studies with temporal comparisons.

^B Indicates studies with both spatial and temporal comparisons.

^W Indicates study conducted in winter.

^{NP} Indicates studies with no statistical analyses or estimate of precision for parameter describing relationship.

^{C1} Pay as cut salvage encouraged limited logging intensity.

^{C2} Abundance estimates were corrected for imperfect detection and relationships with MPB stratified among years. Consequent limits to statistical power may explain why few statistically significant relationships were detected.

^{C3} Although not statistically significant, the relationship had greater negative tendency than found for any other species in the study.

^{C4} Responded positively only to intense logging (50–90% cut), but not moderate logging (15–30% cut).

^{C5} Year effect was significant. In 1 year, red squirrels were more abundant in harvested stands than in uncut forest, but overall mean abundance did not differ among treatment types.

^{C6} More abundant in uncut forest than in any salvage-logged treatment type.

^{C7} More abundant in young pine and single-seed tree than in uncut forest.

^{C8} Study lacks replication; sites were sampled within 2 treatment types, but with no replication across study area.

^{C9} Occupancy estimates were from DNA sampling; differences were primarily caused by higher occupancy by female bears in the logged area versus that in the unlogged area (2.27 times more likely to be found there).

^{C10} Abundance estimates from DNA sampling using detections of unique individuals as an index of abundance.

^{C11} Mortality risk was greater in cutblocks and immature forest stands relative to that for other age classes.

^{C12} Study has no replication; data were collected within 3 treatment types during the outbreak and in a 5-year period pre-MPB, but only one site was surveyed for this study.

^{C13} Use was greatest in uncut forest with MPB, followed by an older clearcut, and least in a salvage-logged block.

after wildfire, entire vegetation communities are affected, and opportunities to retain live trees during postfire salvage logging operations are limited.

The third study was conducted in California where tree harvest included removal of lodgepole pine snags only, while ponderosa pine snags were retained (Kroll et al. 2012). Two studies examined changes in absolute or relative abundance by >20 avian species (Drever and Martin 2010, Kroll et al. 2012), and one examined changes in brood size (number of eggs or nestlings per nest) by six woodpecker species (Edworthy et al. 2011). Another study not reported in our table examined nest survival of nesting assemblages (ground, shrub, and cavity nesters [strong excavators and weak excavators]) but did not provide analyses regarding species-specific responses to salvage logging (Kroll et al. 2010). Consequently, we did not include this study in our synthesis.

Of the 27 species represented in our review, five woodpecker species in one study and two other species in another study were reported to have positive associations with salvage logging based on point count surveys (Table 5), which do not adequately sample nonsinging woodpeckers (Saab et al. 2005). Nest brood size was not significantly related to salvage logging for any woodpecker species. None of the studies reviewed recorded negative associations by any species. Relationships recorded for most species were nonsignificant.

Three publications described responses of 11 nonavian species to postoutbreak salvage logging; only one of these publications was peer-reviewed (Table 5). Abundance was the most common response type; other relationships noted were number of animal locations, occupancy, and mortality risk. Sampling was most commonly conducted through trapping stations. Most studies reported both spatial and temporal comparisons of salvage logging effects on wildlife.

No clear pattern was reported for mammalian associations with postoutbreak salvage logging ($n = 9$ species). Two species, heather vole (*Phenacomys intermedius*) and grizzly bear were reported to have positive associations. Grizzly bear was also reported to have a negative relationship, along with southern red-backed vole (*Clethrionomys gapperi*) and caribou (Table 5). Caribou abundance, measured by the number of radiotelemetry locations, was greatest in uncut forest and least in salvage-logged blocks in British Columbia (Seip and Jones 2009).

In the only peer-reviewed study of the effects of salvage logging on mammals, Sullivan et al. (2010) measured small mammal abundance in relation to four treatment types: (1) young pine (no retention); (2) single-seed tree (dispersed retention); (3) group-seed tree (aggregated retention); and (4) uncut stands. Mean abundance of southern red-backed voles was 2.3–6.4 times higher in uncut stands than in other types, whereas numbers of cinereus shrews (*Sorex cinereus*), northern flying squirrels, and red squirrels did not differ among treatments (Table 5). In contrast, mean abundance of heather vole was significantly greater in the young pine and single-seed tree stands compared with that in uncut stands.

Discussion

Avian Responses

Our review of the literature on avian relationships to MPB epidemics is necessarily coarse in resolution (e.g., we did not distinguish between outbreak size or time since peak of beetle-induced tree mortality); however, we believe that it offers constructive insights. Inconclusive relationships were indicated for many species, but some patterns emerged and were consistent with our predic-

tions. Cavity-nesting species responded more favorably to beetle-killed forests than species with open-cup nests, and species nesting in the shrub layer favored outbreak forests compared with ground and open-cup canopy nesters that generally showed mixed relationships. Bark-drilling species as a group clearly demonstrated a positive short-term association with MPB epidemics compared with that of other foraging assemblages. Contrary to our prediction, bark-gleaning species primarily reliant on live trees were also weakly associated with outbreak forests. Aerial, ground, and foliage-gleaning insectivores and omnivores did not exhibit consistent patterns in relation to beetle-killed forests, and pine seed consumers were seemingly nonresponsive.

The studies reviewed supported our predictions that forest insect outbreaks influence habitat preferences of cavity-nesting birds, particularly bark-drilling specialists (*Picoides* spp.) that rely on beetle larvae as a primary food source (Steeger and Hitchcock 1998, Conner et al. 1999, Norris and Martin 2010). Of the four *Picoides* spp., the black-backed woodpecker showed the weakest positive relationship, particularly in the Rocky Mountain region, whereas the American three-toed woodpecker demonstrated the strongest relationship with MPB outbreaks. This outcome is consistent with the life histories of the two species.

The black-backed woodpecker specializes more on wood-boring beetle larvae (Cerambycidae) than the American three-toed woodpecker, which specializes on bark beetle larvae (Scolytidae) and strongly associates with beetle-killed forests (Murphy and Lehnhausen 1998, Dixon and Saab 2000, Imbeau and Desrochers 2002). Black-backed woodpeckers tend to rely more on recently burned forests rather than on beetle-killed forests in the Rocky Mountain and Inland Northwest regions (Hutto 1995, Saab et al. 2007, Russell et al. 2009b). Consistent with their disturbance-oriented life history, however, black-backed woodpeckers in the Black Hills of South Dakota demonstrate a stronger positive response to MPB outbreaks (Bonnot et al. 2008, 2009). The Black Hills population is isolated and genetically distinct from the Rocky Mountain and Inland Northwest populations (Pierson et al. 2010). This isolation may facilitate local adaptation toward greater dependence on beetle outbreak forests in the Black Hills, where beetle-killed forests may be more readily available within dispersal distances than burned forests.

Cavity-nesting birds that do not consume bark beetles (i.e., secondary cavity-nesting species and nonbark-drilling woodpeckers) also exhibited some positive responses to MPB outbreaks, although not as pronounced or consistent as those of bark-drilling woodpeckers. Various mechanisms may cause positive responses by these species. Secondary cavity nesters may respond positively to increased availability of cavities generated by woodpeckers, although food limitation may complicate these responses (e.g., Norris and Martin 2010). Red squirrels are a key nest predator of cavity-nesting birds (cf. Saab et al. 2011) so declines in their abundance may increase nest survival rates of cavity nesting birds. Finally, we suggest competitive release as a possible mechanism to explain unexpected lagged increases in nest densities for nonbeetle-foraging woodpeckers. During preoutbreak years in our novel study, five woodpecker species nested almost exclusively in aspen trees. When conifer snags became available as a result of the outbreak, nest placement by the three *Picoides* spp. shifted to conifers, whereas sapsuckers and flickers continued to nest at higher densities in aspen patches. Reduced overall woodpecker densities in aspen may have allowed more nest sites and food resources for woodpecker species that remained in

aspen. Our woodpecker nest density results in relation to a MPB epidemic are consistent with those reported in British Columbia (Edworthy et al. 2011), even for those species that infrequently forage on MPB larvae and nest predominantly in aspen (i.e., red-naped sapsucker and northern flicker). This pattern, observed in two different systems, suggests an ecological cascading effect of MPB disturbance (i.e., release of competitive pressure in aspen forests by beetle-foraging specialists) that ultimately benefits entire woodpecker assemblages. The benefits of this competitive release are probably time sensitive and may only be realized over the short term (within 6 years of the peak in beetle-killed tree mortality).

Most shrub-nesting species exhibited positive or nonsignificant responses, with fewer species responding negatively. We expected both shrub and ground nesters to be nonresponsive in the early years after peak tree mortality because of little change in the understory vegetation, whereas we anticipated these groups to respond positively during the postepidemic period (>6 years after peak tree mortality), as time allowed for development of shrubs and ground vegetation (Page and Jenkins 2007). Many of the positive responses were recorded in both time periods, i.e., during and after the epidemic period (Stone 1995, Drever and Martin 2007, Mosher 2011). Authors identified three ground-to-shrub nesting species with less well-defined associations with beetle-killed forests (both pre- and postepidemic periods), including Swainson's thrush (*Catharus ustulatus*), chipping sparrow (*Spizella passerina*), and dark-eyed junco (*Junco hyemalis*). Changes in ground and shrub vegetation in relation to the beetle outbreaks could have resulted in positive responses by these avian species. Outbreak relationships with the understory were not reported by most authors, but Stone (1995) reported positive relationships with understory biomass and plant species diversity.

Bark insectivores (both bark drillers and bark gleaners) are generally year-round residents; this group could be expected to show both numerical and functional responses to MPB outbreaks (Crawford et al. 1990, Stone 1995). Mountain pine beetles provide bark insectivores with increased food supplies (developing larvae underneath bark in winter and emerging adults in summer), thereby potentially increasing survival and subsequent population densities (cf. Norris and Martin 2010). Nevertheless, all bark insectivores reviewed in this study nest in cavities, which potentially confers benefits during MPB outbreaks (see above). Identifying the mechanisms behind responses by bark insectivores will probably require focused study (e.g., Norris and Martin 2010). Regardless, results from both published studies and our novel data were consistent with our understanding of the ecology of these species.

Although we predicted that foliage gleaners and pine seed consumers would respond negatively to outbreak forests, their relationships were mixed and nonsignificant, respectively. Several studies were conducted at locations where other live conifers were available as foraging substrate for foliage-gleaning insectivores. Furthermore, most studies were conducted during the epidemic period at a time when residual pine cones probably provided a seed source. Consideration of multiple biotic and temporal factors (e.g., time since and severity of disturbance) (Saab and Powell 2005) is needed to fully understand the ecological consequences of beetle outbreaks for wildlife.

Our literature summary suggested some differences in wildlife relationships with MPB outbreaks between lodgepole pine- and ponderosa pine-dominated forests. The studies reviewed reported fewer negative relationships for birds in ponderosa forests, although

the frequency of positive relationships was similar. The trend for cavity-nesting species and bark insectivores mirrored the suggested trend for birds overall. Limited data, however, temper our inferences regarding responses in ponderosa pine-dominant versus lodgepole pine-dominant forests. Furthermore, we cannot address differences in relationships between forest types for nonavian species. Given the potentially important implications of differing disturbance regimes among pine-dominated forest types (lodgepole, ponderosa, and five-needled pines) (e.g., Schoennagel et al. 2004), additional data are needed to effectively guide forest and wildlife management. Understanding how and why wildlife responses differ among forest types could also help us predict wildlife responses to changing disturbance regimes expected as a result of climate change (e.g., Keane et al. 2011).

Results were inconclusive for total bird abundance and species richness in relation to MPB outbreaks, as we predicted. These metrics are not particularly informative ecologically or for conservation of diverse avian communities with a wide array of life history characteristics.

Mammalian Responses

Responses of mammals to MPB outbreaks were mixed, not surprisingly given the dearth of published information. We found merely three studies (only one peer-reviewed publication) addressing mammalian responses to MPB outbreaks (Drever and Martin 2007), limiting our inferences. In recently beetle-killed forests, some patterns emerged for species associated with forest canopies (e.g., red squirrel). For small mammal species associated with forest understories, however, responses may be more influenced by the postepidemic period (>6 years after peak of beetle-induced tree mortality) when snags fall to produce coarse woody debris.

No relationships were reported between small mammals and MPB-killed trees; however, red-backed vole abundance showed a pattern with respect to coarse woody debris in the understory (Chalfoun and Heyward, unpubl. data). No voles were observed at sites with less than 0.2% coarse woody cover, after which densities increased until reaching a possible plateau at approximately 1% coarse woody material. Our results were consistent with previous studies documenting red-backed vole sensitivity to the amount and distribution of coarse woody debris in the understory (Keinath and Hayward 2003, Ucitel et al. 2003, Vanderwel et al. 2010). These data suggested a threshold relationship such that forest patches with less than a minimal amount of coarse woody debris did not support vole populations. Interpretation of these patterns in the context of MPB-affected stands may therefore rest in part on the relationship between MPB-induced tree mortality and the amount of resulting coarse woody debris on the forest floor (Klutsch et al. 2009).

Red squirrel responses to MPB epidemics were evaluated more often than those of other mammal species. Red squirrels rely primarily on live trees for food and nesting and are typically restricted to forests with seed production; thus, their populations are predicted to be affected negatively by high tree mortality (Koprowski 2005). Consistent with this expectation, results from our novel data and previous studies reported apparent negative effects of beetle-induced tree mortality on red squirrels (Matsuoka et al. 2001, Drever and Martin 2007). Red squirrels may occur more frequently in areas with more live trees because such areas provide more food resources (i.e., greater seed production) and higher canopy cover, which may facilitate evasion of raptor predators (Zugmeyer and Koprowski

2009b). Given their importance as nest predators in forested ecosystems (e.g., Tewksbury et al. 1998), negative responses by red squirrels could positively influence avian nest survival and populations. Habitat use by the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), however, was not affected by beetle-induced forest changes until tree mortality exceeded 64% (Zugmeyer and Koprowski 2009a, 2009b). In contrast, average percent mortality for all tree species and size classes in our novel study, in which we recorded a negative response, was only 24%. Differential responses to tree mortality among studies may be influenced by differences in age structure and species composition of the remaining live trees. Forests with multiple tree species, some of which are nonhosts of MPBs, may allow persistence of red squirrel populations even in areas where MPBs are active.

A caveat to the apparent pattern for red squirrels concerns the potential role of detecting individuals. The three studies that reported negative relationships (two published and one novel) analyzed either apparent occupancy or apparent abundance without accounting for potential effects of MPBs on species detection. In contrast, the only study that accounted for detection (Mosher 2011) reported a negative relationship with detection but no change in occupancy. Red squirrels may be more visible to observers in beetle-killed forests because of greater illumination afforded by a reduced canopy. Alternatively, negative relationships with detection could reflect declines in abundance even if occupancy is not affected (Royle and Nichols 2003). Many reported relationships for other species in the studies reviewed also fail to account for detection probability. Further examination of the interrelationships between detection and observed demographic patterns for wildlife would better illustrate the effects of MPBs.

The effects of spruce beetle outbreaks on mammals could largely mimic those of MPB outbreaks because of common ecological mechanisms (cf. Werner et al. 2006). Patterns of mammalian responses to spruce beetle outbreaks could therefore supplement the literature on mammalian responses to MPB outbreaks in the context of affecting forest management. Regrowth may occur more quickly in MPB outbreaks, given the warmer climates in which these occur versus those for spruce outbreaks. Consequently, the temporal extent of mammalian responses may differ in beetle-killed pine versus spruce forests, even if responses are similar in direction.

Salvage Logging

In our review, the impacts of postoutbreak salvage logging recorded for most avian species were nonsignificant. Importantly, retention of tree species other than lodgepole pine was a vital component of harvest prescriptions described by all three studies (Drever and Martin 2010, Edworthy et al. 2011, Kroll et al. 2012). In British Columbia, retention of Douglas-fir and especially aspen trees was probably essential to maintaining avian habitat in postoutbreak salvaged forests (Drever and Martin 2010, Edworthy et al. 2011). In California, the design of postoutbreak salvage logging included retention of all ponderosa pine snags (Kroll et al. 2012). Aspen and ponderosa pine trees are particularly valuable to many wildlife species, especially cavity-nesting birds, for nesting, foraging, and other life history requisites (e.g., Dobkin et al. 1995, Bull et al. 1997). By retaining these two tree species, the negative effects of postoutbreak salvage logging appeared minimal for avian communities in the studies reviewed. In contrast, the negative effects of postfire salvage logging on bird communities are well documented (e.g., Hutto and Gallo 2006, Saab et al. 2007).

Salvage logging operations are highly variable, and details of harvest and retention must be known to fully understand the impacts of either postfire or postoutbreak logging (cf. Saab et al. 2007, 2009). Notably, disturbance by wildfire affects entire vegetation communities, whereas beetle infestations are directed at host-tree species of usually large diameter (Jenkins et al. 2014). Consequently, the opportunities to salvage log multiple tree species and probable impacts on wildlife are greater after wildfire (e.g., Hutto and Gallo 2006, Saab et al. 2009) than after beetle infestations. Selective harvest of snag species with lesser value (i.e., lodgepole pine) to wildlife may further reduce the impacts of postoutbreak salvage logging (e.g., Drever and Martin 2010, Edworthy et al. 2011, Kroll et al. 2012).

Mammalian associations with salvage logging were primarily nonsignificant or inconclusive. The only peer-reviewed study that examined mammal responses to postoutbreak salvage logging revealed marked negative responses by southern red-backed voles (Sullivan et al. 2010). Responses by this species supported the author's hypothesis that abundance would increase with higher levels of green tree retention. The southern red-backed vole is associated with late successional coniferous forests and thus would be expected to decline with logging (Sullivan et al. 2010). Influences of small-scale management activities, such as salvage logging, are difficult to assess for wide-ranging mammals, such as grizzly bear or caribou. Nevertheless, several reports have speculated on the negative effects of salvage logging on these species (Munro et al. 2008, Seip and Jones 2009) and empirical studies are needed. Mixed responses by grizzly bears reported by Munro et al. (2008) suggest opposing impacts on different population parameters. Occupancy estimates of bears after a MPB outbreak were greater in salvage-logged versus unlogged forests, as measured with DNA sampling. The bears were negatively affected, however, by postoutbreak salvage logging as measured by mortality risk.

Forests affected by large-scale disturbances of insects and fire have become more prevalent and are expected to increase with climate change, allowing more opportunities for salvage logging in the future. Land managers must balance removal of MPB-killed trees for timber and fuels reduction with habitat requirements for wildlife species associated with snags. Wildlife habitat suitability varies across postepidemic conditions; thus, a need to identify and retain areas of high suitability (refugia) for populations relying on this ephemeral resource exists.

Knowledge Gaps, Research Needs, and Management Relevance

Publications describing avian responses to MPB outbreaks were far more common than those for mammalian responses (16 studies and 89 species versus 6 studies and 11 species, respectively). Within these two vertebrate classes, we did not find published studies specifically designed to evaluate the influence of broad-scale regional changes from MPB outbreaks on vertebrate species that require large landscapes for their population persistence (e.g., grizzly bears, Canadian lynx [*Lynx canadensis*], wolverine [*Gulo gulo*], gray wolf [*Canis lupus*], Northern goshawk [*Accipiter gentilis*], spotted owl [*Strix occidentalis*]). Uncertainty exists about whether these wide-ranging carnivores have the potential to compensate for landscape changes in forest conditions by moving to other areas (cf. Noss et al. 2002).

Evidence suggests that MPB-induced tree mortality might positively affect small mammal populations by producing coarse woody

debris on the forest floor, a key component of small mammal habitat. Coarse woody debris could represent an indirect pathway by which insect infestations influence small mammals in post-MPB outbreak landscapes, especially as time progresses. We recommend continued examination of small mammal demographic relationships with MPB mortality while simultaneously measuring critical microhabitat features, such as coarse woody debris, that potentially modulate these relationships.

Among all vertebrate classes, knowledge gaps regarding the effects of MPB outbreaks and corresponding changes in habitat quality and quantity are greatest for reptiles and amphibians. We found no publications describing herpetofauna and the effects of MPB outbreaks during our searches. Bunnell et al. (2004) evaluated the potential effects on vertebrates, including reptiles and amphibians, of salvage logging in forests affected by MPBs. They hypothesized that large-scale removal of cover might adversely affect western toads (*Anaxyrus boreas*), but with retention of some trees and maintenance of riparian areas, effects could be minimal. Empirical examination of demographic responses by herpetofauna to MPB outbreaks, including evaluation of predictions inferred from habitat-based studies, is sorely needed.

Because controlled experiments to evaluate the effects of large-scale insect outbreaks are not possible, observational studies are essential for understanding the ecological consequences of landscape-altering beetle disturbances. All observational studies to date have been conducted in either lodgepole pine or ponderosa pine. There is a clear need to examine wildlife population changes in relation to beetle outbreaks in forests dominated by other pine species, particularly whitebark pine and other five-needled pines in subalpine forests that are increasingly being affected by beetle outbreaks (Logan et al. 2010, Loehman et al. 2011). Also evident from this review is the need for consistency in reporting the severity of beetle disturbance (e.g., percent beetle-induced tree mortality), time since the peak of beetle-induced tree mortality, and approximate area affected by beetle disturbance. Reporting these standard metrics would allow future reviewers to conduct more informative analyses examining variation in wildlife responses to different MPB outbreaks.

We also lack information on the fitness consequences of beetle-induced forest change. Studies to date emphasize occupancy or abundance relationships. Fewer studies examine MPB relationships with demographic parameters that drive population change (e.g., fecundity) (Bonnot et al. 2008, Saab et al. 2011), limiting our understanding and ability to make predictions.

Some authors have developed models that quantify habitat relationships, in which they predict the effects of MPB outbreaks on wildlife (e.g., Proulx 2009, Steventon and Daust 2009). Validation of these models with empirical data, especially for nonavian species, would greatly enhance our understanding about the effects of MPB outbreaks on wildlife. Similarly, many studies and reviews report the effects of MPB outbreaks on vegetation structure and composition and allude to potential effects on wildlife habitat but lack empirical data on wildlife use or demographic parameters in relation to MPB outbreaks (e.g., Chan-McLeod and Bunnell 2003, Klenner and Arsenault 2009).

A better understanding of MPB-wildlife relationships is especially necessary for ecologists to determine the effects of climate change and consequent changes to disturbance regimes (e.g., Proulx 2009, Steventon and Daust 2009). Habitat suitability models provide a promising tool for examining likely species distribution re-

sponses to spatially and temporally dynamic climate-landscape interactions arising from rapid and unprecedented changes in climate (e.g., Larson et al. 2004, Keith et al. 2008, McRae et al. 2008). These interactions will probably cause significant shifts in plant species composition and disturbance regimes and thus distributions of suitable habitat for wildlife (Millar et al. 2007). Linkages among various simulation modeling platforms will be necessary to explore interactions of climate, vegetation, and fire (e.g., FireBGC model; Keane et al. 2011) with MPB population dynamics (e.g., Powell and Bentz 2009) and with wildlife habitat suitability (e.g., Larson et al. 2004). Probably as a result in part to a lack of data describing current disturbance-related habitat distributions, studies examining probable wildlife responses to changing disturbance regimes are relatively uncommon (cf. Larson et al. 2004, Shifley et al. 2006).

Forests affected by multiple interacting disturbances, including MPB outbreaks, present unprecedented challenges for managing secondary effects on fuels and wildlife habitat. Clear positive responses to MPB outbreaks by cavity-nesting birds and avian bark-drilling species suggest wildlife reliance on these ephemeral habitat conditions. Recently disturbed forests may function as critical source habitats for some wildlife species (cf. Saab et al. 2011). Management of postoutbreak forests should include retention of suitable habitat for such species, particularly for disturbance specialists that rely on habitats created by forest insect outbreaks (e.g., the American three-toed woodpecker). In forests composed of multiple tree species (e.g., both conifer and aspen), selective harvest of tree species least valuable for wildlife (e.g., lodgepole pine while retaining ponderosa pine and aspen) may maintain suitable habitat for many avian (Drever and Martin 2010, Edworthy et al. 2011, Kroll et al. 2012) and mammalian species (Sullivan et al. 2010, this study [red squirrel data]).

Forests dominated by ponderosa pine are the target of most forest restoration activities in the western United States (e.g., Hessburg et al. 1999, Allen et al. 2002, Baker et al. 2007) as a consequence of the close proximity of these forests to urban development. Objectives of the restoration activities include reducing the risks of beetle outbreaks and fires, which can potentially benefit or harm wildlife. Ponderosa pine forests characterized by high basal area, stem densities, and stand densities of large diameter trees (>25 cm dbh) are particularly vulnerable to MPB infestation (Negron and Popp 2004, Negron et al. 2008). Large diameter ponderosa pine trees also are favored by many wildlife species (e.g., Bull et al. 1997, Rabe et al. 1998, Tiedemann et al. 2000, Saab et al. 2009). Implementing forest restoration activities while also meeting the requirements of existing laws to maintain wildlife habitat will require tools for predicting potential wildlife habitat changes in landscapes affected by climate change, MPB outbreaks, and other disturbances. Monitoring wildlife populations and their habitat is essential to implementing adaptive management for meeting both forest restoration and wildlife conservation goals.

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Tree mortality after synchronized forest insect outbreaks: Effects of tree species, bole diameter, and cutting history



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ABSTRACT

A recent series of bark beetle outbreaks in the Rocky Mountain region of the U.S. is the largest and most intense ever recorded. Factors contributing to tree mortality from bark beetles are complex, but include aspects of forest stand condition. Because stand conditions respond to forest management, evaluating bark beetle-caused tree mortality and changes in forest structural attributes in areas previously subjected to management not only improves mechanistic understanding of beetle-caused changes in forests, but also improves prediction of future bark beetle responses to management regimes. We retrospectively assessed mortality of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), and stand structure in two watersheds in south-central Wyoming, U.S.A. following outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*), and western balsam beetle (*Dryocoetes confusus*). One watershed received 240 patch cuts (mean area 1.5 ha), a type of group selection cut, six years before the beetle outbreaks began; the other watershed received no active management (control). We conducted surveys of forest vegetation attributes over 27 yrs, during pre-harvest, post-harvest, and post-outbreak periods. After the outbreak, lodgepole pine and Engelmann spruce mortality increased with increasing bole diameters and basal area of each species, but patterns of mortality were influenced by patch-cutting. Large-diameter trees in or near patch cuts tended to escape attack by bark beetles. Away from patch cuts (≥ 15 m), mortality of smaller lodgepole pine was higher compared to the control watershed. Based on our observed patterns of tree mortality, we hypothesize a changing pattern of host selection (i.e., selection for smaller trees) was influenced by stand conditions that created more suitable conditions for bark beetles in areas between patch cuts in the treated watershed. Snag density increased from pre-harvest to post-outbreak periods, but log density was similar, suggesting most dead trees remained standing at the time of data collection. Canopy cover did not decrease as expected, and ground cover did not change substantially from pre-harvest to post-outbreak periods. Patch-cutting improved survival probability of large-diameter lodgepole pine and Engelmann spruce during outbreaks of multiple species of bark beetle, although reduced losses were only realized for trees in or near (≤ 15 m) patch cuts. However, during intense, broad-scale tree mortality events, these benefits may be important in reducing the loss of mature trees to bark beetles and promoting retention of a larger cohort of mature trees post-outbreak.

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1. Introduction

Bark beetles, a group of species naturally occurring in coniferous forests of North America, are an important source of habitat modification and heterogeneity in these ecosystems (Schowalter

et al., 1981; Franklin et al., 2007). Bark beetle outbreaks, under certain conditions, can result in high tree mortality over extensive areas, leading to cascading changes in structure or species composition of forests (Veblen et al., 1991). Outbreaks can also affect nutrient cycling and hydrologic processes, including water quality (Coulson and Stephen, 2006). Forest vertebrates can also be affected, via changes in resource availability or habitat selection (Martin et al., 2006; Saab et al., 2013). Specifically, insectivores may experience short-term surges in food availability, canopy-sensitive species may be negatively affected a few years after tree

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death, and species associated with abundant logs may find favorable conditions 1–3 decades following the infestation. Beetle-caused tree mortality presents major management challenges in terms of fire risk, hazard trees, and timber production (Samman and Logan, 2000). These challenges may result in significant economic consequences due to altered forest management prioritizing trail and road clearing, or changes in wood fiber characteristics affecting potential wood products for many decades. Therefore, studies of the magnitudes of beetle infestations relative to host species, tree size and cutting history are needed.

During the past two decades conifer forests in the Rocky Mountains experienced one of the most intense and extensive beetle-caused tree mortality events ever recorded. Forests of nearly every coniferous type from New Mexico to British Columbia have been affected. Multiple species of bark beetle have been involved. In Colorado and Wyoming, the primary species have been mountain pine beetle (MPB: *Dendroctonus ponderosae* Hopkins) and spruce beetle (*Dendroctonus rufipennis* Kirby), and to a lesser extent, western balsam beetle (*Dryocoetes confuses* Swaine; Raffa et al., 2008; Bentz et al., 2009). A disturbance of this magnitude necessarily motivates a broad range of ecological and management questions related to bark beetles. These beetle species largely kill individual trees within mature forest stands at low rates during most years but extensive forest mortality events, like that observed recently in the Rockies, occur episodically (Raffa et al., 2008). Except during the most severe outbreaks, small trees are rarely attacked or killed by these species of bark beetles (Bleiker et al., 2003; Fettig et al., 2007). For instance, MPB attack lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) trees <10 cm diameter at breast height (dbh; Roe and Amman, 1970; Shore et al., 2006) at much lower rates than larger trees, demonstrating the influence of individual tree characteristics on bark beetle activity. However, the susceptibility of individual trees >10 cm dbh may differ as a function of stand condition, topography, elevation, tree vigor, weather, and climate, at local and regional scales. Stands with greater tree density or basal area have been shown to be at greater risk of attack by beetles, and risk of attack increases with stand age, percentage of host type, and in stands with a high proportion of large diameter trees (Christiansen et al., 1987; Fettig et al., 2013). Otherwise susceptible stands may resist attack and suffer low tree mortality during years of above-average precipitation indicating the importance of climate in broad-scale mortality events (Chapman et al., 2012; Raffa et al., 2008). Furthermore, brief weather events can have dramatic influence on tree mortality – extreme winter cold that extends over several weeks may significantly reduce beetle-caused tree mortality for several years (Macias Fauria and Johnson, 2009).

Partial cutting in systems dominated by lodgepole pine and ponderosa pine (*P. ponderosae* Dougl. Ex Laws.) has effectively reduced mortality rates from MPB (MacGregor et al., 1987; Amman et al., 1988; Schmid and Mata, 2005). Similarly, mortality from spruce beetles was significantly reduced in stands of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) treated with partial-cutting (Hansen et al., 2010). Therefore, partial cutting has emerged as a potential tool for reducing total tree mortality in landscapes at risk for infestation. However, the efficacy of partial cutting in reducing bark beetle-caused mortality may be influenced by remaining levels of growing stock, patterns of tree grouping, stand structure, and landscape context, as well as beetle demography and behavior (Olsen et al., 1996; Schmid and Mata, 2005; Fettig et al., 2007). Structural characteristics in post-harvest stands can influence microclimate, which is perhaps even more important than structural characteristics *per se* because it strongly affects beetle behavior and whether a suitable host tree is attacked (Bartos and Amman, 1989). In managed stands, bark beetles may be deterred by microclimate features such as warmer temperatures, lower humidity, and higher wind speeds than in unmanaged

stands. These factors may inhibit larval development or the spread of pheromone plumes used to coordinate tree attacks with other individuals (Amman and Logan, 1998; Thistle et al., 2004). Thus, an evaluation of specific partial cutting techniques is essential to determine how overall tree mortality rates may be affected.

Beginning in approximately 1996, MPB populations erupted in north-central Colorado and south-central Wyoming (Harris et al., 2001). Since approximately 2005, MPB populations have been at epidemic levels in mountains of southern Wyoming (Harris, 2006). As of 2012, over 1.7 million ha of pine (*Pinus* spp.) – dominated forests in south-central Wyoming and Colorado had been affected by this series of outbreaks (Harris, 2013). Additional outbreaks of other bark beetle species occurred concurrently with the initial MPB outbreak. Spruce beetle activity began with a large blowdown event in 1997 near Steamboat Springs, Colorado. As of 2012, spruce beetles had affected >420,000 ha in south-central Wyoming and Colorado. In the same region, western balsam bark beetle, a species implicated in mortality of subalpine fir, had affected >95,000 ha (Harris et al., 2001, USDA Forest Service, <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/>).

The occurrence of these bark beetle outbreaks in two watersheds where pre-outbreak data on forest structure and composition were collected presented the opportunity to evaluate whether patch-cutting, a type of group selection cut, influenced subsequent tree mortality or stand structure. Our objectives were to compare changes in tree mortality and structural attributes over time between patch-cut and uncut stands in treatment and control watersheds. We also tested for the previously demonstrated relationship between basal area and mortality rate of the same species. We include pre-epidemic data to evaluate whether changes in forest characteristics caused by the beetle epidemic were affected by forest management.

2. Materials and methods

2.1. Study site

Our study was conducted in the Sierra Madre Mountains of south-central Wyoming, in the Medicine Bow National Forest near the town of Encampment. Mean annual temperature during the period 1982–1986 was estimated to be 1 °C, and ranges from –10 °C in January to 12.9 °C in July. Mean annual precipitation is 87 cm, about 70% of which falls as snow (Bevinger and Troendle, 1987).

The study site comprised the Coon Creek and adjacent East Fork, Encampment River (“East Fork”) watersheds (Fig. 1). These watersheds were the site of a water yield augmentation project, begun in 1985 and completed in the 1990s, designed to evaluate the efficacy of one timber harvest technique to increase surface water yield at the scale of large basins (Troendle et al., 2001). Paired watersheds covering 1673 ha (Coon Creek) and 908 ha (East Fork) were selected based on similar size, aspect, elevation, and timber cover. Mean aspect for Coon Creek is 266° and for East Fork is 197°, and elevation for both watersheds ranges between 2682 and 3322 m (Troendle et al., 2001). During 1990–1992, 240 small patch cuts (mean area 1.5 ha; range: 0.1–7.0 ha) were created in Coon Creek while East Fork remained untreated. Within Coon Creek, a 985-ha portion considered to be the sampling area received 155 patch cuts and a system of access roads (total length = 31.5 km). Within patch cuts, most trees >15 cm dbh were removed, leaving fewer than 10 trees/ha (Hayward et al., 1999). Some advanced regeneration was retained, but as much as 95% of volume was removed. Patch cuts were distributed uniformly throughout the treated area, resulting in cut areas that were 53 m from the nearest neighbor, on average (Troendle et al., 2001). Prior to harvest, both watersheds

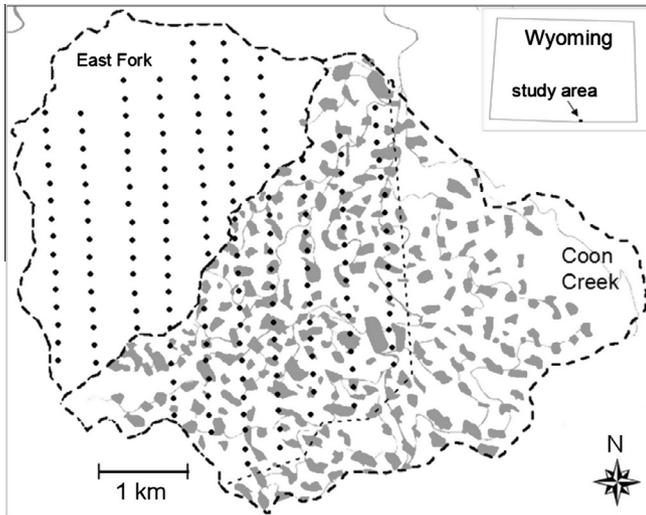


Fig. 1. Watershed boundaries (thick dashed line) for the control (East Fork) and treatment (Coon Creek) watersheds and location of 180 plots used for vegetation surveys (black dots) in south-central Wyoming, USA. Plots are 200 m apart along north-south transects, and transects are 400 m apart. The thin dashed line delineates the portion of the treatment watershed that was sampled during vegetation surveys. Dark gray areas indicate patch cuts and roads.

were dominated by lodgepole pine (60%) and Engelmann spruce-subalpine fir (40%) cover types, and 70% of the forest was categorized as mature (Raphael, 1988). About 3.2% of the areas of both watersheds were natural openings; after harvest, 23% of the treatment watershed (22% of the sampled area) was in patch cuts. Cuts occurring in spruce-fir were smaller than those in lodgepole pine to allow for site protection, and all uncut areas were at least as large as cut areas. Cover types were cut in similar proportions to those available (χ^2 Goodness of fit = 5.2, d.f. = 4, $P=0.26$), and 70% of the patch cuts occurred in areas dominated by lodgepole pine that was >41 cm dbh (USFS E. O'Doherty, unpublished data).

Foliage color and retention can be used as a course indicator of length of time since beetle attack, and thus the approximate stage of the beetle epidemic (Safiranyik et al., 1974; Klutsch et al., 2009). In both watersheds in 2011, 43% of all lodgepole pine had green foliage (indicating the tree was still alive), 7% had red foliage (indicating the tree was attacked within the last 2 yrs), and 49% of trees were gray (indicating the tree was attacked >2 yrs prior and most foliage had fallen off). Fifty-four percent of all Engelmann spruce had green foliage, <1% had red or yellow foliage, and 46% were gray. Seventy-one percent of subalpine fir had green foliage, <2% had red foliage, and 27% were gray (Johnson and Buskirk, unpublished data). Color assessments were made visually in the field. The low proportion of lodgepole pine in the red phase and high proportion in the gray phase suggest mountain pine beetle activity may have been largely completed in these two watersheds by 2011. Additionally, mountain pine beetle populations were reported to have declined locally, impacting fewer acres in south-central Wyoming in 2012 than 2011 (Harris, 2013). Spruce beetle activity was also likely complete in our watersheds given our observed patterns of foliage color, and aerial survey reports that spruce beetle activity decreased from 2011 to 2012 on the Medicine Bow National Forest. Western balsam bark beetle activity was considered moderate, but increased from 2011 to 2012 (Harris, 2013, USDA Forest Service, <http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/>).

2.2. Data collection

In each watershed, 90 permanent sampling points were systematically placed from a random start at 200-m intervals along

north-south transects 400 m apart (Fig. 1). Sampling points were established prior to any harvesting activities. Vegetation surveys were conducted at sampling points in 1985 (pre-harvest), 1992 (post-harvest), 2011, and 2012 (both years representing post-outbreak conditions). Observers measured a distance of 11.3 m and 15 m from each point in four cardinal directions and marked the boundaries of the plot with survey flags. In the treatment watershed observers recorded whether any part of the 15-m plot fell within a patch cut; if so, the plot was designated a "patch-cut" plot; if not the plot was designated an "uncut" plot. All plots within the control watershed were designated as "control" plots. All vegetation data were collected within the boundaries of the 11.3-m-radius (0.04-ha) plot. Because sampling point locations were designated before cutting took place, part of the 0.04-ha plots designated as "patch-cut" often included portions that were not cut, but laid adjacent to a cut (Fig. 1).

In 1985, 1992, and 2011, cover percentages were estimated visually for shrubs, grasses/sedges ("grasses"), and forbs. Number of snags (trees that were dead and ≥ 20 cm dbh and ≥ 2 m tall) and logs (≥ 20 cm diameter at 1.5 m from large end, ≥ 2 m long, and $\geq 10\%$ within the 0.04-ha plot) were counted. Canopy cover was estimated using the average of one reading taken in each cardinal direction at the boundary of each plot using a spherical densiometer. Basal area for each tree species was estimated using a metric relascope in 1985 and 1992, and using a wedge prism relascope in 2011.

In 2012, observers used the same 0.04-ha plots to refine estimates of tree mortality by species and size class. All trees >1.4 m tall were counted, identified to species, assigned to one of nine size classes (≤ 10 , 11–15, 16–20, 21–30, 31–40, 41–50, 51–60, 61–70, or ≥ 71 cm dbh), and assigned a status of live or dead. Live trees were identified as having a canopy mostly comprised of green foliage; dead trees were identified as those not meeting the green foliage requirement and within any stage of decomposition but still standing.

2.3. Statistical analysis

Mortality rates for each tree species were compared using mixed effects analysis of variance in Program SAS (V. 9.3), where treatment (control, treatment uncut, and treatment cut) was modeled as a fixed categorical effect, total basal area of each species was modeled as a fixed continuous effect, and individual plot was a random effect. We also tested for effects of treatment \times total basal area to address the question of whether the effect of total basal area differed depending on proximity to timber harvest. We evaluated changes in vegetation characteristics over time using mixed effects repeated measures analysis of variance with year as the repeated variable. Covariance structure for measurements among time periods was initially unknown, and our five candidate models included: compound symmetry, unstructured, autoregressive, heterogeneous autoregressive, and autoregressive moving average covariance structures. We calculated the most appropriate model covariance structure and improved model fit by comparing models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002). Response variables were transformed when necessary to meet assumptions of normality and homogeneity of variance. We used Tukey's method to control for Type I error probability when making multiple comparisons among control, uncut, and patch-cut plots for stand structure variables. However, formal hypothesis testing of all possible pairwise comparisons of tree mortality that included all nine size classes would have resulted in an adjusted alpha-level that was too restrictive. Thus, for tree mortality rates we compared degree of overlap of 95% confidence intervals among treatments within a size class to identify which size class categories drove differences

among treatments. The probability that a tree was dead in each size class and treatment was estimated using logistic regression, where size class was treated as an ordinal variable. A Wald test was then used to test the significance of treatment variables. Means are presented \pm standard error.

3. Results

3.1. Tree mortality

For lodgepole pine, average mortality rate ranged from 3% for trees <10 cm dbh in patch cuts to nearly 100% for trees >30 cm dbh in either watershed (Fig. 2). Lodgepole pine mortality for all size classes pooled differed among treatments ($F = 27.65_{2,176}$, $P < 0.0001$). Mortality was similar between control ($42.7 \pm 2.8\%$) and uncut plots ($36.7 \pm 3.9\%$), but was lower in patch-cut ($11.7 \pm 4.2\%$) compared to control ($t = 6.08$, $P < 0.0001$) and uncut plots ($t = 4.27$, $P < 0.0001$). Differences in lodgepole pine mortality among treatments reflected lower mortality for trees ≤ 10 cm dbh in patch cuts than in control and uncut plots, as well as for trees 21–30 cm dbh compared to uncut plots (Fig. 2). While the pattern of lower mortality in patch cuts did not hold for trees 31–40 cm dbh, variation was high for mortality in this size class in patch cuts. However, mortality was 0% for pines in the largest size classes (51–70 cm dbh) in patch cuts. Total basal area (expressed as m^2 per 0.04 ha) of lodgepole pine affected mortality rate ($F = 16.82_{1,176}$, $P < 0.0001$); the relationship was positive ($\beta = 0.01$, $t = 4.10$, $P < 0.0001$; Fig. 3). This relationship was similar across treatments. The probability of a lodgepole pine dying depended on size class and treatment, but generally increased with tree size ($\chi^2 = 72.5$, d.f. = 2, $P < 0.0001$; Table 1).

For Engelmann spruce, mortality rates varied from 2% for trees <10 cm dbh to near 100% for trees >40 cm dbh in both watersheds (Fig. 2). Spruce mortality for all size classes pooled differed among treatments ($F = 22.57_{2,176}$, $P < 0.0001$). Mortality was similar between control ($27.9 \pm 2.3\%$) and uncut plots ($23.0 \pm 3.2\%$), but was lower in patch cut ($9.5 \pm 3.5\%$) compared to both control ($t = 4.38$, $P < 0.0001$) and uncut plots ($t = 2.79$, $P = 0.02$). Total basal area of Engelmann spruce affected mortality rate ($F = 53.70_{1,176}$, $P < 0.0001$), and the relationship was positive ($\beta = 0.03$, $t = 7.33$, $P < 0.0001$; Fig. 3). This relationship was similar across treatments. The probability of an Engelmann spruce dying depended on size class and treatment, but generally increased with size ($\chi^2 = 26.1$, d.f. = 2, $P < 0.0001$; Table 1).

In the case of subalpine fir, average mortality varied from 6% for trees <10 cm dbh in uncut plots of the treatment watershed, approaching 40% for trees >40 cm dbh in the control watershed (Fig. 2). However, mortality was generally lower for trees >40 cm dbh than for lodgepole pine or Engelmann spruce. Although overall mortality differed among treatments ($F = 3.53_{2,176}$, $P = 0.03$), mortality was similar among control ($11.3 \pm 1.6\%$), uncut ($17.0 \pm 2.2\%$), and patch cut ($12.1 \pm 2.4\%$) plots after adjustments for multiple pairwise comparisons. Total basal area of subalpine fir affected mortality rate ($F = 35.66_{1,176}$, $P < 0.0001$) and the relationship was positive ($\beta = 0.02$, $t = 5.97$, $P < 0.0001$; Fig. 3). This relationship was similar across treatments. The probability of a subalpine fir dying was similar among size classes and treatments ($\chi^2 = 1.8$, d.f. = 2, $P = 0.40$).

Mean snag density (for all species combined) depended on year and treatment (year \times treatment interaction: $F = 22.57_{4,177}$, $P < 0.0001$; Table 2). In control plots, snag density was similar pre-harvest to post-harvest, but was higher post-outbreak compared to both pre-harvest (mean difference: 5.5 ± 0.5 snags; $t = 10.94$, $P < 0.0001$) and post-harvest (mean difference: 5.0 ± 0.5 snags; $t = 9.57$, $P < 0.0001$). In the treatment watershed, snag

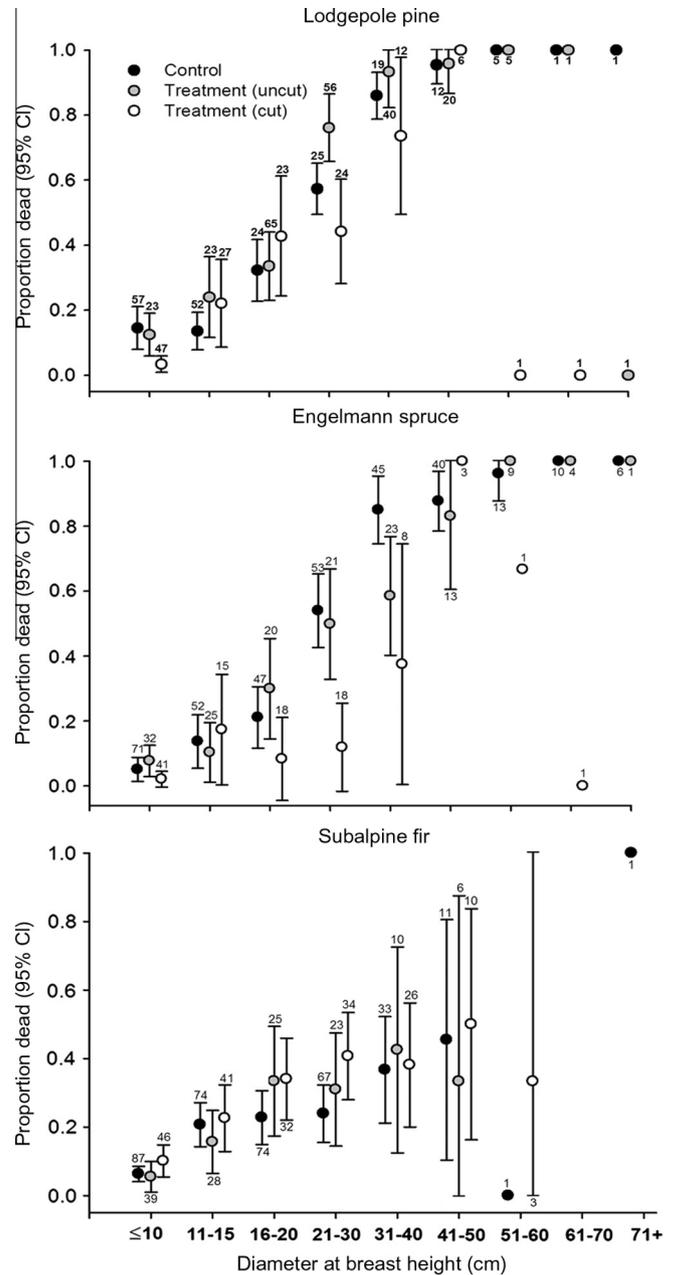


Fig. 2. Lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) mortality by size class and patch cutting treatment (control: sampling points located in the control watershed; treatment [uncut]: sampling points located between patch cuts in the treatment watershed; treatment [cut]: sampling points with any part of the 0.04-ha plot located within a patch cut in the treatment watershed). Error bars are 95% confidence intervals and numbers above or below data point indicate number of sampling points with trees in the respective size class. Data are from two watersheds in the Sierra Madre Range, south-central Wyoming, USA.

density in uncut plots was similar between pre-harvest and post-harvest, but was higher post-outbreak compared to both pre-harvest (mean difference: 6.1 ± 0.7 snags; $t = 9.55$, $P < 0.0001$) and post-harvest (mean difference: 5.9 ± 0.7 snags; $t = 8.79$, $P < 0.0001$). In cut plots, snag density was similar between pre-harvest and post-harvest and between pre-harvest and post-outbreak, but was lower post-outbreak than post-harvest (mean difference: 1.0 ± 0.8 snags; $t = -3.21$, $P = 0.04$).

Canopy cover depended on year and treatment (year \times treatment interaction: $F = 47.36_{4,177}$, $P < 0.0001$; Table 2). In control plots, canopy cover was similar between pre-harvest and post-harvest, but

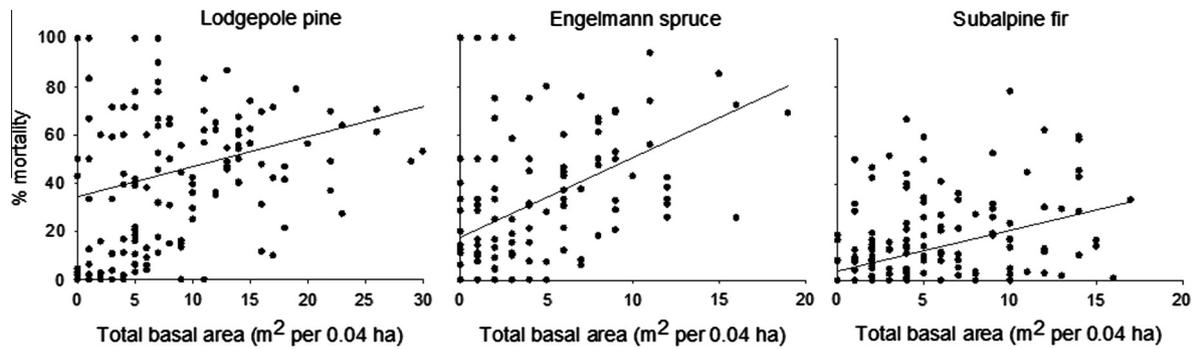


Fig. 3. Mortality rates of three tree species in relation to total (live and dead) respective basal area in south-central Wyoming. Lines represent predicted values from a mixed model with fixed effects of total basal area and treatment, and a random effect of sampling plot. Points where total basal area = 0 but mortality >0% represent sampling artifacts: basal area (BA) was estimated using a wedge prism relascope and where trees were few, BA was estimated as 0. However, mortality rates were estimated by counting all stems within a plot, so trees that were excluded while measuring BA were included in mortality counts.

Table 1
Probability of mortality (95% confidence intervals) for subalpine forest after a broad-scale bark beetle outbreak in the Sierra Madre range, south-central Wyoming. Size classes are based on diameter at breast height (dbh). Trees >60 cm dbh were encountered too infrequently to include in our analysis; however, mortality for this size class approached 100% (Fig. 2). Size class/treatment/species categories too sparsely encountered to allow estimation of probabilities of mortality are indicated by “–”.

| Treatment | Size class (cm) | Probability of mortality | | |
|-----------|-----------------|--------------------------|------------------|------------------|
| | | Lodgepole pine | Engelmann spruce | Subalpine fir |
| Control | ≤10 | 0.13 (0.10–0.15) | 0.04 (0.03–0.07) | 0.07 (0.05–0.08) |
| Control | 11–15 | 0.20 (0.15–0.25) | 0.13 (0.08–0.19) | 0.19 (0.16–0.23) |
| Control | 16–20 | 0.35 (0.29–0.41) | 0.30 (0.22–0.40) | 0.28 (0.24–0.34) |
| Control | 21–30 | 0.64 (0.59–0.68) | 0.59 (0.52–0.66) | 0.28 (0.23–0.33) |
| Control | 31–40 | 0.89 (0.83–0.93) | 0.90 (0.83–0.95) | 0.37 (0.27–0.48) |
| Control | 41–50 | 0.96 (0.88–0.99) | 0.90 (0.82–0.95) | 0.45 (0.25–0.66) |
| Control | 51–60 | – | 0.95 (0.73–0.99) | – |
| Patch cut | ≤10 | 0.01 (0.00–0.02) | 0.02 (0.01–0.06) | 0.04 (0.03–0.06) |
| Patch cut | 11–15 | 0.22 (0.14–0.31) | 0.14 (0.07–0.26) | 0.28 (0.21–0.37) |
| Patch cut | 16–20 | 0.50 (0.40–0.60) | 0.06 (0.01–0.20) | 0.15 (0.09–0.25) |
| Patch cut | 21–30 | 0.62 (0.53–0.70) | 0.11 (0.04–0.27) | 0.20 (0.11–0.34) |
| Patch cut | 31–40 | 0.79 (0.67–0.88) | 0.41 (0.21–0.65) | 0.57 (0.23–0.86) |
| Patch cut | 41–50 | – | – | – |
| Patch cut | 51–60 | – | 0.67 (0.15–0.96) | – |
| Uncut | ≤10 | 0.16 (0.12–0.20) | 0.11 (0.08–0.19) | 0.09 (0.07–0.11) |
| Uncut | 11–15 | 0.24 (0.19–0.30) | 0.21 (0.14–0.30) | 0.30 (0.25–0.36) |
| Uncut | 16–20 | 0.43 (0.37–0.50) | 0.34 (0.24–0.45) | 0.38 (0.30–0.47) |
| Uncut | 21–30 | 0.74 (0.69–0.79) | 0.54 (0.44–0.63) | 0.45 (0.37–0.53) |
| Uncut | 31–40 | 0.96 (0.89–0.99) | 0.64 (0.51–0.75) | 0.46 (0.32–0.61) |
| Uncut | 41–50 | 0.94 (0.69–0.99) | 0.82 (0.57–0.94) | 0.40 (0.16–0.70) |
| Uncut | 51–60 | – | – | – |

increased by $21.5 \pm 2.3\%$ from pre-harvest to post-outbreak ($t = 6.59$, $P < 0.0001$) and by $23.4 \pm 1.5\%$ from post-harvest to post-outbreak ($t = 10.19$, $P < 0.0001$). In the treatment watershed, canopy cover in uncut plots was similar from pre-harvest to post-harvest, but increased by $17.7 \pm 3.0\%$ between pre-harvest and post-outbreak ($t = 3.35$, $P = 0.03$) and by $19.7 \pm 2.8\%$ from post-harvest to post-outbreak ($t = 4.56$, $P < 0.001$). In cut plots, canopy cover decreased by $65.4 \pm 3.0\%$ from pre-harvest to post-harvest ($t = -15.31$, $P < 0.0001$), and by $42.2 \pm 3.3\%$ from pre-harvest to post-outbreak ($t = -8.87$, $P < 0.0001$), but increased by $65.8 \pm 2.3\%$ from post-harvest to post-outbreak ($t = 7.16$, $P < 0.0001$).

3.2. Ground cover

Log density (mean number of logs per 0.04-ha plot) depended on year and treatment (year \times treatment interaction: $F = 6.24_{4,177}$, $P = 0.0001$). In control plots, log density decreased by an average of 5.1 ± 0.7 from pre-harvest to post-harvest ($t = -7.44$, $P < 0.0001$) and by an average of 5.3 ± 0.7 between pre-harvest and post-outbreak ($t = -7.51$, $P < 0.0001$; Table 2). In the treatment watershed, log density in uncut plots decreased by 9.3 ± 0.9 from pre-harvest to post-harvest ($t = -10.18$, $P < 0.0001$)

and by 9.0 ± 1.0 from pre-harvest to post-outbreak ($t = -9.43$, $P < 0.0001$), post-harvest to post-outbreak. In cut plots, log density decreased by an average of 8.5 ± 1.0 from pre-harvest to post-harvest ($t = -8.29$, $P < 0.0001$) and by 10.3 ± 1.1 from pre-harvest to post-outbreak ($t = -9.65$, $P < 0.0001$). Log density was similar between post-harvest and post-outbreak for all plot types, demonstrating that most dead trees resulting from the beetle epidemic were still standing at the time of data collection.

Percent shrub cover depended on year and treatment (year \times treatment interaction: $F = 15.32_{4,177}$, $P < 0.0001$). In control plots, shrub cover was similar among all three time periods (Table 2). In the treatment watershed, shrub cover decreased in uncut plots by $16.7 \pm 2.5\%$ from pre-harvest to post-harvest ($t = -6.76$, $P < 0.0001$), was similar between pre-harvest and post-outbreak, and increased by $18.0 \pm 2.5\%$ from post-harvest to post-outbreak ($t = 7.13$, $P < 0.0001$). In cut plots, shrub cover decreased by $23.4 \pm 2.8\%$ from pre-harvest to post-harvest ($t = -8.50$, $P < 0.0001$) and by $17.6 \pm 2.6\%$ from pre-harvest to post-outbreak ($t = -6.69$, $P < 0.0001$), but remained similar between post-harvest and post-outbreak. Percent forb cover depended on year and treatment (year \times treatment interaction: $F = 16.57_{4,177}$, $P < 0.001$). In control plots, forb cover was similar

Table 2

Mean (95% confidence intervals) values for vegetation attributes at 0.04-ha plots in subalpine forest stands during three time periods (pre-harvest = 1985; post-harvest = 1992; post-outbreak = 2011) in south-central Wyoming, USA.

| | 1985 | | 1992 | | | 2011 | | |
|---------------------------------------|------------------|------------------|------------------|-------------------|------------------|------------------|-------------------|------------------|
| | Control | Treatment | Control | Treatment (uncut) | Treatment (cut) | Control | Treatment (uncut) | Treatment (cut) |
| Snag density | 2.0 (1.6–2.5) | 1.9 (1.5–2.3) | 2.5 (1.9–3.1) | 2.6 (1.7–3.4) | 2.4 (1.7–3.0) | 7.5 (6.5–8.5) | 8.4 (7.3–9.4) | 0.9 (0.4–1.4) |
| Log density | 10.8 (9.5–12.2) | 15.9 (14.1–17.6) | 2.5 (2.0–4.1) | 3.0 (1.5–3.7) | 8.0 (6.1–9.9) | 7.5 (6.3–9.0) | 8.3 (5.1–9.8) | 6.4 (4.8–7.9) |
| Canopy cover | 65 (61–69) | 68 (64–71) | 64 (60–67) | 69 (65–73) | 24 (19–30) | 79 (76–81) | 78 (74–81) | 39 (33–46) |
| Percent shrub cover | 46.4 (41.6–51.3) | 47.7 (42.6–52.9) | 40.9 (36.6–45.3) | 28.3 (22.7–33.8) | 26.7 (22.1–31.3) | 42.0 (36.9–47.0) | 46.0 (39.0–52.4) | 32.9 (27.4–38.5) |
| Percent forb cover | 10.8 (7.3–14.3) | 9.5 (5.5–13.4) | 8.1 (5.9–10.3) | 7.7 (4.3–11.1) | 1.4 (1.1–1.8) | 8.3 (6.0–10.5) | 10.6 (6.9–14.4) | 7.8 (6.2–9.4) |
| Percent grass cover | 13.1 (8.5–17.8) | 8.5 (4.4–12.6) | 11.2 (7.4–15.0) | 8.0 (3.6–12.4) | 2.3 (1.0–3.7) | 13.4 (9.9–16.9) | 11.3 (6.6–16.0) | 14.9 (10.2–19.5) |
| Percent total vegetation cover | 64.4 (60.5–68.2) | 61.7 (57.1–66.2) | 60.2 (57.2–63.3) | 43.9 (37.5–50.4) | 30.4 (25.9–35.0) | 63.6 (60.0–67.2) | 67.5 (62.5–72.5) | 55.6 (50.5–60.7) |
| Percent lodgepole pine ^a | 49.0 (42.4–55.7) | 54.3 (46.9–61.6) | 46.4 (39.9–52.9) | 46.5 (35.9–57.1) | 41.9 (31.7–52.1) | 44.0 (37.1–50.1) | 48.1 (37.2–59.0) | 41.1 (28.8–53.4) |
| Percent Engelmann spruce ^a | 24.7 (19.4–30.1) | 21.2 (16.1–26.4) | 24.4 (19.2–29.6) | 26.1 (18.7–33.6) | 14.4 (8.3–20.5) | 22.1 (17.1–27.1) | 25.9 (18.5–33.2) | 19.5 (11.0–28.0) |
| Percent subalpine fir ^a | 26.2 (22.1–30.3) | 24.5 (20.2–28.9) | 29.2 (25.0–33.4) | 27.4 (21.2–33.7) | 34.4 (25.8–43.0) | 32.9 (28.1–37.7) | 25.7 (19.1–32.2) | 31.9 (22.6–41.2) |

^a Percent of total basal area (live + dead) for each species.

among years. In the treatment watershed, forb cover in uncut plots was similar from pre-harvest to post-harvest and from pre-harvest to post-outbreak, but increased by 3.3% between post-harvest and post-outbreak ($t = 4.72$, $P < 0.0001$). In cut plots, forb cover was similar from pre-harvest to post-harvest, but increased by 4.7% from pre-harvest to post-outbreak ($t = 6.83$, $P < 0.0001$), and by 6.4% from post-harvest to post-outbreak ($t = 10.06$, $P < 0.0001$; Table 2). Percent grass cover depended on year and treatment (year \times treatment interaction: $F = 15.63_{4,177}$, $P < 0.0001$). In control plots, grass cover was similar between pre-harvest and post-harvest and pre-harvest and post-outbreak, but increased by $2.2 \pm 1.2\%$ from post-harvest to post-outbreak ($t = 3.21$, $P = 0.04$). In the treatment watershed, grass cover in uncut plots was similar between pre-harvest to post-harvest and pre-harvest and post-outbreak, but increased by $3.6 \pm 1.6\%$ from post-harvest to post-outbreak ($t = 3.16$, $P = 0.05$). In cut plots, grass cover was similar from pre-harvest to post-harvest, but increased by $12.9 \pm 2.2\%$ from pre-harvest to post-outbreak ($t = 10.28$, $P < 0.0001$) and increased by $13.0 \pm 1.8\%$ from post-harvest to post-outbreak ($t = 9.93$, $P < 0.0001$).

Total vegetation ground cover (shrub + forb + grass cover) depended on year and treatment (year \times treatment interaction: $F = 20.33_{4,177}$, $P < 0.0001$). In control plots, total vegetation cover was similar among all years. In the treatment watershed, total vegetation cover in uncut plots decreased by $23.4 \pm 2.5\%$ from pre-harvest to post-harvest ($t = -9.44$, $P < 0.0001$), increased by $24.8 \pm 2.5\%$ from post-harvest to post-outbreak ($t = 9.93$, $P < 0.0001$), but was similar between pre-harvest and post-outbreak (Table 2). In cut plots, total vegetation cover decreased by $25.8 \pm 2.8\%$ from pre-harvest to post-harvest ($t = -9.37$, $P < 0.0001$), and increased by $25.3 \pm 2.8\%$ from post-harvest to post-outbreak ($t = 9.09$, $P < 0.0001$). Total vegetation cover was similar between pre-harvest and post-outbreak in uncut and cut plots.

4. Discussion

Tree mortality patterns after recent synchronized bark beetle outbreaks were influenced by tree species, bole diameter, and cutting history. Mortality was highest for lodgepole pine and Engelmann spruce, while subalpine fir experienced generally lower mortality. Mean mortality rates tended to increase with size class and basal area for lodgepole pine and Engelmann spruce, but varied widely for subalpine fir in larger size classes. At the lowest

values of basal area, mortality rate of subalpine fir was less than 10%. Surprisingly, canopy cover increased, and coarse woody debris remained similar from pre-outbreak to post-outbreak time periods. Ground vegetation cover did not change markedly from pre-outbreak to post-outbreak time periods, with the exception that grass cover increased in patch cuts.

A potential limitation of our study is that we did not identify specific agents of tree mortality. However, attributing tree mortality to specific causes was not the primary focus of our study. Given the size and intensity of the ongoing bark beetle epidemic in the region and patterns we assessed while making field observations, we are comfortable assuming a relatively large proportion of tree mortality was caused by bark beetles. However, we emphasize that this report is of the status of Rocky Mountain subalpine forest before and after a major bark beetle event that occurred across the region, but our patterns of tree mortality reflect the results of multiple threats occurring coincidentally. Furthermore, these patterns of tree mortality associated with historical management have been retrospectively assessed. The study design did not originally include questions regarding beetle-induced tree mortality, thus providing limited potential to infer which processes produced the patterns we observed.

Higher mortality of larger trees is expected during outbreaks of mountain pine beetle, spruce beetle, and western balsam beetle, because larger trees are preferentially attacked by these species (Schmid and Frye, 1976; Geiszler and Gara, 1978; Bleiker et al., 2003). However, cutting history at our study site influenced mortality rates in unexpected ways. In patch cuts, mortality of lodgepole pine tended to be lower for several size classes than in uncut areas of the treatment watershed or the control watershed, suggesting patch cutting may benefit trees located close (≤ 15 m) to cuts during bark beetle outbreaks. Indeed, in patch cuts, trees in the largest size classes had no mortality (Fig. 2). Uncut areas between patch cuts in the treatment watershed (>15 m away from a patch cut) generally had similar mortality rates for lodgepole pine as the control watershed for all size classes pooled, but evaluating patterns within each size class reveals an exception for trees 21–30 cm dbh. Trees in this size class located between patch cuts experienced higher mortality than trees of similar size in the control watershed (Fig. 2). We hypothesize that this pattern reflects the effect of the spatial distribution of suitable and unsuitable conditions on bark beetle behavior in the treatment watershed. Bark beetle activity tends to be greater near trees with closed canopy where temperature, light intensity, and wind speed remain at optimum levels (Bartos and Amman, 1989), characteristics which are

likely met in uncut plots but less so in patch cuts. Further, host trees of preferred sizes are located closer to each other in uncut plots than in and around patch cuts, and thus may be easier for bark beetles to locate. When the first few individuals attack a tree, those individuals emit an aggregating pheromone that attracts other individuals to the same tree. Once the tree's defenses have been overcome, individuals emit a disaggregating pheromone which repels additional individuals (Raffa et al., 2008). Individuals repelled from the focal tree should attack suitable trees nearby, producing a clustering effect on mortality that has been shown in other studies (Preisler, 1993; Safranyik and Carroll, 2006; Progar et al., 2013). The patch cuts in the treatment watershed may have increased the patchiness of the microclimates suitable for beetle activity, and concentrated beetles in areas away from patch cuts, leading to higher mortality among slightly smaller trees in areas between patch cuts than in the control watershed. A similar pattern was not observed in the control watershed where suitable microclimates and host trees are more evenly distributed across the watershed.

Other investigators have observed comparable patterns in which tree selection by bark beetles varied over the course of an outbreak (Klein et al., 1978; Amman and Cole, 1983). In these studies, selection for smaller-diameter trees increased as the pool of large-diameter available host trees declined. Here we present evidence consistent with this changing pattern of host selection on a spatio-temporal scale. At our study site, some large-diameter host trees near patch cuts—trees of the size class that would have been preferred early in the outbreak—escaped attack by beetles, presumably because they were less likely to be encountered. We hypothesize that this occurred because the low density of large-diameter trees in patch cuts led to a lack of signals from beetles in the area that large trees were available. Thus, from a beetle's perspective, perceived host depletion may have occurred more quickly in areas near patch cuts, forcing beetles to select smaller host trees in areas farther from patch cuts with high mean densities of trees of suitable diameter.

Patterns of mortality for Engelmann spruce were generally similar to those for lodgepole pine, and trees in most size classes seemed to benefit from being located in or near patch cuts. Group tree selection methods, including patch-cutting, are commonly used to facilitate Engelmann spruce regeneration in the central Rockies. These methods result in stands with higher species and age-class diversity, which are less susceptible to direct bark beetle attack, but may also indirectly aid suitable hosts in avoiding attack by making them less obvious to beetles (Price, 1997; Fettig et al., 2007).

Patterns of mortality for subalpine fir differed from that of the other tree species studied. While the positive relationship with basal area was similar to other species, overall mortality was lower and did not differ among control, uncut, and patch cut plots. Further, the relationship between dbh and mortality was weak. Although initial attacks by western balsam bark beetles may not result in mortality, the beetles can introduce the fungus *Ceratocystis dryocoetidis*, which can increase the susceptibility of the tree to subsequent beetle attacks, both of which may ultimately result in mortality (Molnar, 1965; Garbutt, 1992). Further, subalpine fir mortality in the region of our study area has been attributed to a combination of root disease caused by *Armillaria* spp. or *Heterobasidium* spp. and western balsam bark beetle activity, collectively known as “subalpine fir decline” (Harris et al., 2001; Harris, 2012). Limited data are available on bark beetle-caused mortality of true fir (Fettig et al., 2007), but studies by Bleiker et al. (2003) and McMillin et al. (2003) suggest that mortality patterns are similar to other tree species that host bark beetles: larger trees with reduced vigor are more susceptible to attack. However, because mortality often occurs in conjunction with other factors such as

blow-down events and root and fungal disease, mortality patterns of subalpine fir at our study site may reflect more complicated dynamics than just initial stand and tree conditions.

Although mortality rates differed slightly for some species and size classes, stand conditions following the outbreaks were similar between plots in the control watershed and uncut plots in the treatment watershed. Further, differences in stand conditions between patch-cut plots and control or uncut plots were largely restricted to snag and log density, and we found few substantial differences in ground cover by 10 yrs post-harvest. However, as more snags fall and coarse woody debris on the forest floor increases over time, important differences in ground cover between patch-cut and other treatments may become apparent.

Our observation of increased canopy cover from pre-outbreak to post-outbreak periods was unexpected. This result is likely a function of increased stand age over time, but may also reflect the use of a spherical densiometer to quantify canopy cover. We recognize the weaknesses associated with spherical densimeters (Cook et al., 1995). However, so that our data could be compared to historical data recorded at the study site, we opted to use the same method to measure canopy cover. Because most dead trees were still standing at the time of data collection, substantial decreases in canopy cover likely have not yet occurred. Although needle loss from the canopy has occurred, densimeters may not have the sensitivity required to capture such fine-scale changes in canopy cover.

5. Conclusions

Patch-cutting in subalpine forest appears to have improved survival probability among lodgepole pine and Engelmann spruce during a synchronized bark beetle outbreak, although reduced losses to bark beetles were only realized for trees in or near patch cuts. However, during intense, broad-scale events with mortality of some size classes approaching 100% like that occurring at our study site, these benefits may be important in reducing the loss of mature trees to bark beetles and promoting retention of a larger cohort of mature trees after the outbreak. Thus, patch-cutting executed under multiple forest management goals, including reducing bark beetle-caused mortality, should be considered as a measure offering partial protection from mortality within the context of the extent and intensity of the beetle outbreaks and proximity of focal trees to patch cuts.

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1 TIMBER HARVEST INTERACTS WITH CLIMATE-ASSOCIATED FOREST MORTALITY
2 TO INFLUENCE POPULATION DYNAMICS OF A VERTEBRATE SEED PREDATOR

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35 Abstract

36 The mechanisms by which climate change may affect vertebrates include direct effects of altered
37 temperature and precipitation regimes, but also indirect effects mediated by disturbance. Broad-
38 scale disturbances have the potential to interact with habitat heterogeneity produced by previous
39 disturbances, thus contributing to variation in the response of vertebrates to climate change.
40 Recent and current outbreaks of bark beetles (including *Dendroctonus* spp. and *Dryocoetes*
41 *confuses*) in the Rocky Mountains have resulted in an opportunity to investigate effects of
42 climate-associated tree mortality on an important seed predator in coniferous forests, the red
43 squirrel (*Tamiasciurus hudsonicus*), and to evaluate whether those effects interact with forest
44 heterogeneity produced by previous timber harvest. The purpose of our study was to describe
45 site occupancy dynamics for red squirrels in relation to patch-cutting, a type of group selection
46 cut, and the bark beetle outbreak, and to evaluate whether patch cutting influenced subsequent
47 effects of bark beetles on squirrels. We used multi-season occupancy models and covariates
48 quantifying harvest- and outbreak-related habitat characteristics to describe extinction and
49 colonization rates of red squirrels over a 27-yr period in south-central Wyoming, USA. We
50 observed effects of year, patch-cutting, and the bark beetle outbreak on the probability of
51 detecting a red squirrel. We observed a negative association between local extinction rate and
52 increasing snag density, but only to a threshold of 5 snags/0.04 ha. We observed a positive
53 association between local colonization rate and the basal area of live trees. Annual site
54 occupancy varied across years, and was lowest during the period after the bark beetle outbreaks
55 began. Tree mortality tended to be lowest near patch cuts; this pattern was especially
56 pronounced for mature trees (>30 cm diameter at breast height) which tend to produce the most
57 cones and would likely contribute the most to red squirrel survival. The strong habitat effects on

58 occupancy dynamics suggest that previously-harvested areas may provide refugia for red
59 squirrels in post-outbreak forests, and support managing for uneven-aged stands in subalpine
60 forests of the Rocky Mountains.

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81 Keywords: bark beetle; climate change; colonization; disturbance interactions; extinction; forest
82 health; fragmentation; subalpine forest
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104 INTRODUCTION

105 Climate change is predicted to alter biogeography, demography, and life history
106 attributes, extending to species interactions, biodiversity, and ecosystem processes (Parmesan
107 2006, Keith et al. 2008, Peters et al. 2013). The mechanisms by which climate change will
108 influence vertebrates are forecasted to include direct effects of altered temperature and
109 precipitation regimes, and indirect effects mediated by disturbance (Dale et al. 2001). The latter
110 may accelerate species responses to climate-related change. Forest biomes may be particularly
111 susceptible to alteration of disturbance regimes because trees are long-lived, and some tree
112 species are adapted to low disturbance frequencies, with limited capacity to respond to
113 disturbance quickly via dispersal (Dale et al. 2000, 2001). Climate-related disturbance has
114 recently been manifested as large-scale forest mortality events in high-elevation coniferous
115 forests of western North America caused by synchronized outbreaks of several species of bark
116 beetle (Raffa et al. 2008, Bentz et al. 2010).

117 Direct and indirect effects of climate change and land use interact to affect biodiversity
118 (Hansen et al. 2001). Multiple disturbance types (e.g. cutting and herbivory) typically interact
119 with each other and with preexisting habitat heterogeneity (Veblen et al. 1994). Preexisting
120 disturbances can strongly influence the response of a system to subsequent ones, and all of these
121 factors have the potential to contribute to the creation of conditions unique for that site over
122 human history (Turner 2010). For example, trees weakened by recent fire can be more
123 susceptible to subsequent bark beetle attack (McHugh et al. 2003, Kulakowski and Jarvis 2013).
124 In managed forests, salvage logging often follows fire or insect defoliation, and these multiple
125 perturbations may contribute to unique landscape patterns that would not exist in the absence of
126 one of them (Paine et al. 1998, Radeloff et al. 2000).

127 Impacts of climate change on disturbance regimes and interactions among disturbance
128 types will have far-reaching ecological consequences for biodiversity. Knowledge of multiple
129 disturbances on vegetation is relatively well-developed, but our understandings are weak of how
130 higher trophic levels respond to complex disturbances in vegetation. For some groups like small
131 mammals, this knowledge gap is significant because they perform important ecological functions
132 in forest systems. Both red-backed voles (*Clethrionomys* spp.) and flying squirrels (*Glaucomys*
133 spp.) are spore dispersal agents of ectomycorrhizal fungi, and both are important prey for
134 vertebrate predators of western forests (Buskirk and Ruggiero 1994, Powell and Zielinski 1994,
135 Pyare and Longland 2001). The red squirrel (*Tamiasciurus hudsonicus*) is a coniferous forest
136 obligate occurring at densities up to 6.0 individuals/ha (Rusch and Reeder 1978, Sullivan and
137 Moses 1986, Gurnell 1984), and typically associated with mature, seed-producing trees. The
138 species is considered a keystone taxon in Rocky Mountain forests (Pearson and Ruggiero 2001,
139 Smith et al. 2003), because of its roles as predator and prey. Red squirrel consumption of tree
140 buds, young tree stems, and seeds significantly influence lodgepole pine (*Pinus contorta*)
141 reproduction and rates of stand-level cone serotiny (Benkman and Siepielski 2004; Talluto and
142 Benkman 2013). Further, predation of bird nests by red squirrels is thought to strongly influence
143 canopy-nesting bird communities in conifer forests (Siepielski 2006). Red squirrels are prey for
144 the Northern Goshawk (*Accipiter gentilis*; Squires 2000), martens (*Martes* spp.; Buskirk and
145 MacDonald 1984), Canada lynx (*Lynx canadensis*; Koehler and Aubry 1994), and Great Gray
146 Owl (*Strix nebulosa*; Schauffert et al. 2002). Squirrel food caches and associated deposits of
147 cone bracts, called middens, are exploited by various mammals, including bears (Mattson and
148 Reinhardt 1997), other squirrels, voles, and mice for food, and martens for resting or foraging
149 (Pearson and Ruggiero 2001). Thus, many of the features of late-successional Rocky Mountain

150 subalpine forests, from perspectives of conifer life history and wildlife habitat, are mediated over
151 ecological or evolutionary time scales by red squirrels.

152 Beginning around 1996, mountain pine beetle (MPB: *Dendroctonus ponderosae*
153 Hopkins) populations in Colorado erupted and the outbreak expanded northward into Wyoming
154 (Harris et al. 2001). From around 2005, MPB populations have been at epidemic levels in
155 mountains of southern Wyoming, and additional species of bark beetles, including the spruce
156 beetle (*Dendroctonus rufipennis* Kirby) and western balsam beetle (*Dryocoetes confuses* Swaine)
157 concurrently expanded their populations. By 2012, over 17,000 km² of pine (*Pinus* spp.) –
158 dominated forests in Colorado and Wyoming had been affected, resulting in mortality rates
159 approaching 100% for lodgepole pine and Engelmann spruce >30 cm in diameter at breast height
160 (dbh) in subalpine forest of south-central Wyoming (Harris 2013; Johnson et al. 2014). This
161 outbreak over the last ~ 17 years affected an historical study site where experimental timber
162 harvest and its effects on vertebrates were intensively studied during 1985 – 96. The data from
163 before and after cutting--but before the bark beetle outbreak--provided an opportunity to evaluate
164 possible interactions between beetle-caused tree mortality and previous timber harvest, along
165 with the demographic response of an ecologically important mammalian species that is closely
166 associated with large-diameter conifers.

167 From the same study area, we earlier reported that large diameter (>50 cm dbh) lodgepole
168 pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*) located near areas harvested
169 15-20 years earlier had high probabilities of survival after the bark beetle outbreak. However, in
170 areas at least 15 m away from areas previously harvested, mortality was higher for lodgepole
171 pine in smaller size classes, suggesting landscape characteristics created by pre-outbreak harvest
172 may influence bark beetle activity (Johnson et al. 2014). Contrary to our predictions in that

173 study, we observed increases in canopy cover from the 1980s to the post-outbreak period. We
174 expected these characteristics to influence the abundance and distribution of red squirrels at our
175 study site. In addition to snag density and canopy cover, the amount of live basal area could
176 influence red squirrel populations because it represents local capacity for conifer seed
177 production.

178 Here, we report site-occupancy dynamics in relation to forest stand characteristics for a
179 population of red squirrels in south-central Wyoming, USA. Changes in vital rates of red
180 squirrel populations are indicated by local extinction and colonization events, two of the
181 mechanisms by which species respond to climate change (Hansen et al. 2001). The bark beetle
182 outbreak allowed us to evaluate effects of tree mortality on red squirrel site occupancy, and to
183 determine whether site occupancy dynamics differed between areas previously exposed vs. not
184 exposed to timber harvest. We expected that the harvested watershed would show reduced red
185 squirrel densities in the three years of study following cutting, because of the removal of cone-
186 producing trees and destruction of middens. Because beetle kill is concentrated in large-diameter
187 conifers, we expected that regenerating lodgepole pine would not be killed outright by beetles,
188 and that any indirect effect of beetles on red squirrels in the harvested watershed would be
189 additive to that caused by cutting. Density of snags, basal area of live trees, and canopy cover
190 might plausibly predict the occurrence of red squirrels; we tested the predictive power of all
191 three habitat variables.

192 METHODS

193 We collected data to test predictions regarding occupancy, extinction, and colonization of red
194 squirrels in response to changes in habitat from timber harvest and beetle-induced tree death.
195 We included live basal area, snag density, and canopy cover as covariates. The sampling units

196 for occupancy modeling were permanent 100 m-radius plots sampled repeatedly for red squirrels
197 from 1985-1996, then in 2011-2012.

198 STUDY AREA

199 Red squirrel populations were sampled within two adjacent watersheds in the Sierra Madre
200 Mountains of south-central Wyoming, 18 km south of the town of Encampment (Fig. 1).

201 Elevation of the two watersheds ranges from 2682 to 3322 m. Mean annual precipitation was 87
202 cm, 70% of which occurred as snow (Troendle et al. 2001). Snow cover typically lasted from
203 late September to late June. Forest cover was 60% lodgepole pine, and 40% was a mixture of
204 Engelmann spruce and subalpine fir (*Abies lasiocarpa*) cover types. Seventy percent of the
205 forest was characterized as mature during a 1985 vegetation survey (Raphael 1988).

206 *Experimental design*

207 The two watersheds studied were the upper East Fork of the Encampment River (East Fork; 908
208 ha) and Coon Creek (1673 ha). These adjacent watersheds were the site of an experiment during
209 1985-1996 designed to evaluate whether patch-cutting, a type of group selection cut, could
210 increase water yield at the scale of large basins (Troendle et al. 2001). The two watersheds were
211 paired because of their similarity in size, elevation, aspect, and timber cover. Coon Creek, the
212 treatment watershed, received 240 patch cuts (mean area: 1.5 ha; range: 0.1-7.0 ha). A 985-ha
213 area was designated as the portion to be sampled to evaluate wildlife and vegetation responses;
214 this area received 155 patch cuts and a system of access roads (total length = 31.5 km in
215 sampling area, 44.1 km on entire watershed). The pre-harvest period was 1985 – 90, harvest
216 occurred from 1990 – 92, and the post-harvest period was 1993 – 96. East Fork, the control
217 watershed, remained uncut, and contained no roads before or after cutting. The areas compared
218 between the two watersheds were similar in basal area for each cover type, canopy cover, tree

219 height, old growth score, and ground cover types at the beginning of the study (Raphael 1987).
220 About 3.2% of the areas of both watersheds were natural openings; after harvest, 23% of the
221 treatment watershed (22% of the sampled area) was in patch cuts. Cover types were cut in
222 proportions similar to those available (χ^2 Goodness of fit = 5.2, d.f. = 4, $P = 0.26$), and 70% of
223 the patch cuts occurred in areas dominated by lodgepole pine where mean dbh >41 cm (USFS E.
224 O'Doherty, unpublished data). Within patch cuts, most trees >15 cm were removed, but some
225 advanced regeneration was retained, resulting in post cutting densities <10 trees/ha (Hayward et
226 al. 1999).

227 *Squirrel population sampling*

228 In each watershed, 90 permanent sampling points were established in 1985 prior to harvesting.
229 Sampling points were established using a compass and measuring tape and systematic 200-m
230 spacing from a random start. Points were fixed along transect lines that ran north-south and were
231 400 m apart (Fig. 1). Red squirrels were sampled during 5–6 standardized point count surveys
232 conducted each summer from mid-June to late July, distributing sampling effort equally across
233 both watersheds each day. During each survey, an observer walked to the sampling point, waited
234 silently for 1 min, then recorded the number of red squirrels seen or heard within 100 m of the
235 point during a 10-min period. Point count surveys began within 30 min of dawn and were
236 completed before 11:00 MST, and were not conducted during periods of high wind (>15 m/sec)
237 or heavy rain.

238 *Vegetation sampling*

239 Vegetation surveys were conducted in 1985 (pre-harvest), 1992 (post-harvest), 2011, and 2012
240 (both years representing post-outbreak conditions) at the same permanent sampling points where
241 red squirrels were surveyed. Observers measured a distance of 11.3 m and 15 m from each point

242 in four cardinal directions and marked the boundaries of the nested circular plots with survey
243 flags. In the treatment watershed observers recorded whether any part of the 15-m plot fell
244 within a patch cut; if so, the plot was designated a “treatment cut” plot; if not the plot was
245 designated an “treatment uncut” plot. Part of the plots designated as “treatment cut” often
246 included portions that were not cut, but lie adjacent to a cut. All plots within the control
247 watershed were designated as “control” plots. All vegetation data were collected within the
248 boundaries of the 11.3-m-radius (0.04-ha) plot (Fig. 1).

249 To estimate snag density, observers counted all dead trees ≥ 20 cm dbh and at least 1.8 m
250 tall. Trees were considered dead if $< 50\%$ of needles were green and the tree was in any stage of
251 decomposition but still standing. Stand basal area was estimated separately for live and dead
252 trees of each species using a wedge prism relascope and a basal area factor of 10. Canopy cover
253 was measured by taking the average of four readings (one in each cardinal direction) at the
254 boundary of each plot using a spherical densiometer.

255 *Statistical analysis*

256 From our multiple surveys within each year, we created encounter histories for red squirrels at
257 each sampling point during the study period. Each encounter history represented detections
258 during 83 visits to each of 180 sampling points during the entire sampling period. We tested for
259 effects of timber harvest and beetle-kill on site occupancy dynamics by estimating extinction and
260 colonization as a function of treatment (control, treatment uncut, and treatment cut), time, and
261 habitat covariates.

262 We modeled site occupancy using multiple-season probabilistic models developed by
263 MacKenzie et al. (2003, 2006). These models use maximum likelihood estimation to estimate
264 probability of site occupancy when detection probabilities are < 1 , and allow incorporation of

265 effects of time, group effects, and habitat variables (MacKenzie et al. 2002). These models are
266 based on primary sampling occasions (years, which allows estimation of extinction and
267 colonization rates across years) subdivided into secondary sampling occasions (visits to each
268 sampling point within a year, which allows estimation of detection probabilities). Our study
269 included 14 years and 5–6 visits within each year. Sites were assumed open to changes in
270 occupancy status among years, but closed to changes among visits within a single year. Lack of
271 closure among visits within a year was possible; however red squirrels are territorial throughout
272 the year and do not hibernate, so individuals present should have been available for detection
273 during all surveys. Using these models, we estimated the probability of site occupancy (ψ_1) for
274 the initial year, extinction probability (ε) and colonization probability (γ) for each interval
275 between year i and year $i + 1$ (i.e., conditional on status in year i), corrected for the probability of
276 detection (ρ_{ij}) given presence in each survey (j) within a year (t). Estimates of annual site
277 occupancy were derived using the following equation from MacKenzie et al. (2003):

278

$$279 \quad \hat{\Psi}_t = \hat{\Psi}_{t-1}(1 - \hat{\varepsilon}_{t-1}) + (1 - \hat{\Psi}_{t-1})\hat{\gamma}_{t-1} .$$

280

281 We used a multi-stage approach to modeling site occupancy of red squirrels, similar to
282 Olson et al. (2005) and Dugger et al. (2011). First, we modeled detection probability by
283 evaluating constant, annual, and treatment-specific effects. During this stage of modeling, we
284 held site occupancy, extinction, and colonization in their fully-parameterized forms (time \times
285 treatment) to account for maximum variation not associated with detection probability. We
286 included models where detection probability varied before and after timber harvest at sampling
287 points where cutting did and did not occur (within the treatment watershed), and before and after

288 the bark beetle epidemic. Once the best structure for ρ_{ij} was identified, it was retained and used
289 for the remainder of the modeling process. During the second stage of modeling, we evaluated
290 time and treatment effects on extinction and colonization probabilities. Exploratory data analysis
291 suggested initial site occupancy was similar among the three treatment groups; thus we held site
292 occupancy constant during the second stage of modelling. The best model from this stage was
293 retained for the final stage of modeling, where habitat covariates were added to test for effects of
294 snag density, live basal area, and canopy cover. Candidate models that included habitat
295 covariates were based on predicted relationships between habitat variables and red squirrel
296 occupancy informed from established relationships reported in the primary literature. All models
297 were generated and executed using Program MARK (White and Burnham 1999). We used
298 Akaike's Information Criterion corrected for small sample sizes (AIC_c) for model selection at
299 each stage of the modeling process (Burnham and Anderson 2002). Whether 95% confidence
300 intervals for slope coefficients overlapped zero was considered when evaluating the importance
301 of variables in competing models ($<2 AIC_c$). All parameter estimates are presented as mean \pm
302 standard error.

303 RESULTS

304 *Habitat characteristics*

305 We reported earlier that timber harvest and bark beetle activity substantially altered forest
306 characteristics (Johnson et al. 2014), thus potentially affecting habitat for red squirrels. Timber
307 harvest reduced canopy cover by $65.4 \pm 3.0\%$ at harvested plots; however, from post-harvest to
308 post-outbreak, canopy cover at harvested plots recovered, increasing by $65.8 \pm 2.3\%$. Canopy
309 cover increased over the entire study period (pre-harvest to post-outbreak) in control plots (by
310 $21.5 \pm 2.3\%$) and uncut plots in the treatment watershed (by $17.7 \pm 3.0\%$). Harvest did not affect

311 snag density (for all tree species combined), but bark beetle activity increased density of snags
312 by $5.5 \pm 0.5/0.04$ ha at control plots and by $6.1 \pm 0.7/0.04$ ha at uncut plots in the treatment
313 watershed. Snag density was not substantially changed at plots in the treatment watershed that
314 were harvested. The bark beetle outbreak resulted in high mortality of lodgepole pine and
315 Engelmann spruce, and moderate mortality of subalpine fir (Johnson et al. 2014). The total
316 amount of live basal area (TLBA: lodgepole pine + Engelmann spruce + subalpine fir) was
317 similar before and after harvest in the control watershed, and in the treatment watershed at points
318 that were not harvested. At points that were harvested, TLBA decreased from 30.1 ± 1.4 to 14.4
319 ± 2.1 m²/ha from pre-harvest to post-harvest. After the bark beetle outbreak, TLBA was reduced
320 to <10 m²/ha in all treatments (Fig. 2).

321 *Red squirrel detection probabilities*

322 Over the 14 years of our study, we detected red squirrels on 8901 occasions. Of those, 3708
323 (41.7%) occurred in the treatment watershed and 5193 (58.3%) in the control. In the treatment
324 watershed, mean number of detections per year pre-harvest was 183.4 ± 29.1 , post-harvest was
325 372.9 ± 70.7 , and post-outbreak was 90.5 ± 33.5 . In the control watershed, mean number of
326 detections per year pre-harvest was 233.4 ± 24.6 , post-harvest was 549.4 ± 78.8 , and post-
327 outbreak was 90.0 ± 42.0 . Probability of detection varied among treatments and years (Table 1),
328 but was consistently <0.8 (Fig. 3). There was strong support for treatment-and year-specific
329 variation in detection probabilities ($w_i = 1.0$). In the control watershed, detection probabilities
330 ranged from 0.30 ± 0.03 to 0.46 ± 0.03 across sampling sites during the 6-yr pre-harvest phase.
331 During the 6-yr post-harvest phase, detection probabilities ranged from 0.40 ± 0.03 to $0.75 \pm$
332 0.02 . In each post-outbreak year, detection probabilities were 0.15 ± 0.03 and 0.27 ± 0.03 ,
333 respectively. In the treatment watershed, detection probabilities at points in the “treatment cut”

334 category ranged from 0.19 ± 0.03 to 0.45 ± 0.04 pre-harvest. Post-harvest, detection ranged
335 from 0.30 ± 0.05 to 0.62 ± 0.03 , and was 0.21 ± 0.05 and 0.27 ± 0.04 for 2011 and 2012,
336 respectively. In the treatment watershed, detection probabilities at uncut points ranged from 0.13
337 ± 0.03 to 0.47 ± 0.04 pre-harvest, from 0.33 ± 0.04 to 0.66 ± 0.03 post-harvest, and were $0.17 \pm$
338 0.04 and 0.30 ± 0.05 for 2011 and 2012, respectively (Fig. 3).

339 *Occupancy parameters*

340 *Treatment and time effects.*—We found strong support for an effect of year on extinction and
341 colonization rates of red squirrels, but the effect was similar among control, treatment cut, and
342 treatment uncut plots. Our top model garnered strong support as it accounted for 89% of AIC_c
343 weight (Table 2).

344 *Habitat correlates.*—Snag density most strongly affected extinction probabilities for red squirrels,
345 and the relationship included a threshold effect of snag density values (Table 3). This effect was
346 well-supported as all five best models included a threshold effect of snag density (Table 3).

347 Extinction probabilities decreased with increasing snag density at the 0.04-ha scale, but only
348 until density reached 5 snags/0.04 ha ($\beta = -0.22 \pm 0.06$, 95% CI = -0.33 to -0.11 ; Table 3, Fig.
349 4). Live basal area most strongly affected colonization probabilities, and an effect of live basal
350 area was included in three of the four best models (Table 3). Colonization probabilities
351 increased with increasing live basal area ($\beta = 0.03 \pm 0.02$, 0.001 – 0.06; Fig. 5). This model had
352 an AIC_c weight of 0.55 and was almost 3 times more likely than the second-best model. The
353 latter model ($<2 AIC_c$) did not include an effect of any habitat covariate on colonization
354 probabilities (Table 3). Extinction and colonization probability as well as habitat covariate
355 values varied widely from before to after the beetle outbreak; thus, we present the two time
356 periods separately. Mean annual site occupancy was generally high before the bark beetle

357 outbreak, but was highest during and immediately after patch-cutting (Fig. 6). In the two years
358 after the bark beetle outbreak, site occupancy was lower and more variable (Fig. 6).

359 DISCUSSION

360 Our retrospective study included a spatial control only for timber harvest, and took advantage of
361 a natural experiment: a broad-scale bark beetle epidemic that continues through the Rocky
362 Mountains. The strong, positive effect of live basal area on colonization rates suggests that
363 climate-associated tree mortality interacts with timber harvest—in our case patch-cutting—to
364 influence site occupancy dynamics for an important seed predator, the red squirrel. Large (>30-
365 cm-dbh) trees, those trees that typically produce the most cones, near (≤ 15 m) patch cuts had
366 higher probabilities of surviving the bark beetle outbreak than similarly-sized trees farther from
367 patch cuts (Johnson et al. 2014). Regeneration within patch cuts generally resulted in trees
368 smaller in size class than is typically preferred by bark beetles, and mortality in patch cut plots
369 was lower than at uncut plots in the treatment watershed and plots in the control watershed
370 (Johnson et al. 2014). Areas near patch cuts thus had a lower probability of site occupancy
371 shortly after cutting, but regeneration within patch cuts likely served as refugia after the bark
372 beetle outbreak.

373 Estimates of detection probability varied strongly across time and among treatments—
374 from 0.13 to 0.75—showing that detection probability should be considered when inferring
375 abundance of red squirrels. Other authors have observed comparably variable detection
376 probabilities for red squirrels across time (range: 0.03–0.22; Rytwinski and Fahrig 2011). The
377 probability of detection generally increased across all treatments after harvest, which may have
378 been caused by displaced individuals from patch-cut areas prospecting for new territories, but
379 plots that were cut tended to have lower detection rates than control plots until the post-outbreak

380 time period. Similarity in detection probability among treatments after the bark beetle outbreak
381 suggests that tree mortality swamped any effects of previous harvesting and had a homogenizing
382 and depressing effect on detection probability. Many factors may influence detection
383 probability: including abundance, observer attributes, and habitat characteristics. However, red
384 squirrels adjust their behavior in response to local population density, vocalizing less frequently
385 when local densities are low (Dantzer et al. 2012). The majority of detections throughout our
386 study were by call only (79%), suggesting that decreased detection probabilities could be related
387 to decreased population density. A similar pattern of decreased detection probability after beetle
388 outbreak was reported in Montana (Mosher 2011), and decreased detection during the post-
389 outbreak time period could reflect decreased abundance even without large changes in
390 occupancy (Royle and Nichols 2003).

391 The absence of an effect of patch-cutting on site occupancy dynamics was unexpected,
392 given previously documented responses by red squirrels. Koprowski (2005) reported reductions
393 in red squirrel density in both clear-cuts and areas thinned to densities of 500-2304 stems/ha,
394 although squirrel density may remain high in edge habitats and residual corridors between cuts.
395 Comparing these results to those from the stage of our analysis with habitat covariates suggests
396 our treatment classification (i.e. whether any part of the 0.04-ha plot was affected by patch-
397 cutting resulting in a “treatment cut” categorization) did not effectively characterize the
398 treatment. Plots classified as “treatment cut” were sometimes dominated by uncut habitat, and
399 the proportion of plots directly affected by cutting varied widely. So, while we did not detect a
400 treatment effect using group classifications of “cut” – “uncut”, we did observe significant and
401 large treatment effects of the specific structural attributes associated with cutting and our habitat

402 covariates ultimately captured the expected relationship with treatment-related changes in basal
403 area.

404 Site occupancy dynamics were influenced by snag density and live basal area. Snags
405 represent a resource for red squirrels in the form of potential nesting trees (Koprowski 2005), and
406 the threshold relationship with local extinction that we observed suggests that large increases in
407 snag density beyond five snags/0.04 ha did not influence local extinction rates (Fig. 3). The
408 intercept for extinction rates differed markedly from before to after the beetle outbreak,
409 indicating additional variables may have influenced the probability of extinction. However, the
410 beetle outbreak took place at a very broad spatial scale in relation to that at which we sampled,
411 and rates of tree mortality varied spatially and with bole diameter (Johnson et al. 2014). Thus, a
412 lack of snags in our 0.04-ha vegetation plots does not imply a lack of snags within the larger area
413 sampled for squirrel occupancy, and the difference in spatial scale between sampling of
414 vegetation characteristics and of red squirrel occurrence may have influenced the observed
415 change in intercepts among the time periods.

416 The positive relationship between live basal area and colonization rate confirms well-
417 documented habitat requirements for red squirrels. The dependence on conifer cones for food
418 results in positive associations with stand density, tree size, and basal area, because these
419 variables co-vary with seed availability (Zugmeyer and Koprowski 2009). Red squirrels do not
420 specifically require mature forest, but they do require a sufficient element of mature trees to
421 produce seeds for food and to create cool microsites for middens (Koprowski 2005).
422 Regeneration in patch-cut plots was dominated by lodgepole pine, which generally begins cone
423 production within the first ten years, but production of cones approximating mature stand
424 conditions is not reached in southern Wyoming until trees are ≥ 17 cm dbh (50–80 yrs; Koch

425 1996). Thus, re-colonization rates of plots abandoned during cutting were largely influenced by
426 the amount of surrounding forest with mature components. Presumably, post-outbreak
427 regeneration will have a similar influence on re-colonization rates over the coming decades.

428 Site occupancy varied across years, and estimates of site occupancy after the beetle
429 outbreak were within the range of variation of estimates for some years before the outbreak (Fig.
430 6). Red squirrel populations typically vary in size across years, in part because of inter-annual
431 variation in cone production (Gurnell 1984, Dantzer et al. 2012). The magnitude of decrease in
432 annual site occupancy during the post-outbreak period was relatively small; implying that red
433 squirrels are likely to persist through at least the near-term changes in structure and composition
434 predicted for post-outbreak forests. Squirrels may be able to consume seeds from cones on dead
435 trees if seeds are retained in serotinous cones. However, rates of serotiny are low at our study
436 site (78% of plots containing lodgepole pine have rates of serotiny below 10%, Johnson and
437 Buskirk, unpublished data). Over the long term, food diversity provided by multiple conifer
438 species will be important because most conifers mast every 3–6 yrs, and presence of more than
439 one coniferous species provides more consistent cone availability (Silvertown 1980, Hayward
440 2008). Multiple species of bark beetle were active at our study site, and lodgepole pine and
441 Engelmann spruce suffered relatively high rates of mortality (Johnson et al. 2014), suggesting
442 that subalpine fir may be an important resource for red squirrels in the near term. However,
443 subalpine fir also experienced mortality (albeit lower than other conifers) attributed to western
444 balsam bark beetle and root disease caused by *Armillaria* spp. or *Heterobasidium* spp. (Harris et
445 al. 2001, Harris 2012). If these or other mortality agents increase in extent or intensity before
446 lodgepole pine or Engelmann spruce regenerate to a point of sufficient cone production, there
447 could be additional negative consequences for red squirrel populations in the future. Further,

448 patch cuts may become important refugia in the coming decades as regenerating lodgepole pine
449 matures to a point of sufficient cone production.

450 The important role played by red squirrels in food webs of coniferous forests suggests
451 that reduced squirrel abundance may influence other forest species. Red squirrels are important
452 predators of juvenile snowshoe hares (O'Donoghue 1994) and nesting birds (Willson et al.
453 2003), and the predation pressure they exert is a strong influence on avian community
454 composition (Sieving and Willson 1998). Thus, depressed red squirrel abundance may lead to
455 population surges for other community members. Further, reduced seed predation by red
456 squirrels may have implications for changes to forest structure in systems dominated by
457 lodgepole pine. Abundance of red squirrels is negatively related to cone serotiny, and seed
458 predation may overwhelm effects of fire on rates of stand-level serotiny when squirrels are
459 relatively abundant (Benkman and Siepielski 2004, Talluto and Benkman 2013). Coincident
460 bark beetle outbreaks affecting multiple tree species and resulting in prolonged reductions in red
461 squirrel site occupancy or abundance may result in altered spatial variation and reduced intensity
462 of seed predation. If fire-return intervals or fire intensity respond to bark beetle activity in areas
463 of reduced seed predation by red squirrels, stand-level serotiny may increase. Given the
464 important effect of serotiny on post-fire stand density and community structure (Turner et al.
465 1997, Schoennagel et al. 2003), selection imposed by fire and reduced seed predation could
466 influence characteristics across a significant proportion of western North American coniferous
467 forest. Thus, red squirrels may mediate long-term effects of climate change on forest structure,
468 in addition to those directly imposed by tree mortality from bark beetles.

469

470

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472
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650 Table 1. Model selection results for probabilities of detection (p) of red squirrels (*Tamiasciurus*
 651 *hudsonicus*) in the Sierra Madre range, south-central Wyoming, USA (1985-1996, 2011-2012; K
 652 = number of parameters and w = Akaike weight). Initial site occupancy, extinction, and
 653 colonization parameters for all models were held at the most fully-parameterized form.

| p^a | ΔAIC_c^b | K | w | Deviance |
|----------------------------------|------------------|-----|------|----------|
| $p(\text{trt} \times \text{yr})$ | 0.00 | 121 | 1.00 | 17101.56 |
| $p(\text{yr})$ | 115.31 | 82 | 0.00 | 17275.82 |
| $p(\text{trt})$ | 935.69 | 94 | 0.00 | 18121.98 |
| $p(\cdot)$ | 1008.88 | 80 | 0.00 | 18199.45 |

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655 ^a yr = year-specific variation, trt = variation among control, treatment cut, and treatment uncut
 656 plots, \cdot = constant

657 ^b Minimum $AIC_c = 17355.88$

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667 Table 2. Model selection results for models relating year, patch-cutting, and bark beetle activity to extinction (ϵ) and colonization (γ)
668 probabilities for red squirrels in the Sierra Madre range of south-central Wyoming, USA (1985-1996, 2011-2012; K = number of
669 parameters and w = Akaike weight). Year, treatment, and beetle effects were added to a base model that included a constant
670 probability of initial site occupancy [$\psi(\cdot)$] and the best detection probability structure [p (trt \times yr)].

| ϵ^a | γ^a | ΔAIC_c^b | K | w | Deviance |
|------------------------------|------------------------------|------------------|-----|------|----------|
| yr | yr | 0.00 | 69 | 0.89 | 17155.10 |
| yr(beetle.) | yr*trt(beetle.) | 4.26 | 72 | 0.11 | 17153.01 |
| yr*trt(beetle) | yr*trt(beetle) | 10.04 | 77 | 0.01 | 17148.17 |
| yr(beetle.) | yr*trt+beetle | 10.94 | 73 | 0.00 | 17157.57 |
| yr*trt(cut=uncut) | yr*trt(cut=uncut) | 17.88 | 87 | 0.00 | 17134.63 |
| yr*trt(uncut=control) | yr*trt(uncut=control) | 28.14 | 95 | 0.00 | 17127.66 |
| yr*post-trt | yr*post-trt | 28.33 | 97 | 0.00 | 17123.52 |
| yr*trt(pre-1990.: cut=uncut) | yr*trt(pre-1990.: cut=uncut) | 33.10 | 79 | 0.00 | 17166.96 |
| yr*trt (pre-1990.) | yr*trt(pre-1990.) | 33.65 | 77 | 0.00 | 17171.77 |
| yr*trt(pre-1992.: beetle.) | yr*trt(pre-1992.: beetle.) | 39.44 | 69 | 0.00 | 17194.54 |

| | | | | | |
|-------------------|-------------------|--------------|------------|-------------|-----------------|
| yr*trt(pre-1992.) | yr*trt(pre-1992.) | 46.87 | 75 | 0.00 | 17189.25 |
| <u>year*trt</u> | <u>year*trt</u> | <u>55.50</u> | <u>119</u> | <u>0.00</u> | <u>17102.64</u> |

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672 ^a yr = year-specific variation; trt = variation among control, treatment cut, and treatment uncut plots; beetle = effect of beetle kill
673 differed among treatments; beetle. = effect of beetle kill was similar between 2011 and 2012; post-trt = treatment effect only after
674 1990; pre-1990 cut=uncut=control; pre-1990. = constant before 1990 (beginning of harvest), yr*trt effects after 1990; pre-1992. =
675 constant before 1992 (end of harvest), yr*trt effects after 1992.

676 ^b Minimum AIC_c = 17297.04

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686 Table 3. Model selection results for models relating habitat characteristics to extinction (ϵ) and colonization (γ) probabilities of red
687 squirrels in the Sierra Madre range of south-central Wyoming, USA (1985-1996, 2011-2012; K = number of parameters and w =
688 Akaike weight). Habitat characteristics were added to a base model containing year effects on extinction and colonization rates,
689 constant probabilities of initial site occupancy [$\psi(\cdot)$] and the best detection probability structure [p (trt \times yr)].

| ϵ^a | γ^a | ΔAIC_c^b | K | w | Deviance |
|-------------------------------|-------------------------------|------------------------|-----|------|----------|
| yr + snag(T ₅) | yr + liveBA | 0.00 | 83 | 0.55 | 16988.20 |
| yr + snag(T ₅) | yr | 1.99 | 82 | 0.20 | 16992.33 |
| yr + snag(T ₅) | yr + liveBA(T ₂₀) | 3.46 | 83 | 0.10 | 16991.66 |
| yr + snag(T ₅) | yr + liveBA(T ₁₀) | 3.95 | 83 | 0.08 | 16992.15 |
| yr + snag(T ₅) | yr + canopy cover | 4.03 | 83 | 0.07 | 16992.23 |
| yr + snag(T ₁₅) | yr + liveBA | 13.07 | 83 | 0.00 | 17001.27 |
| yr | yr + liveBA | 13.74 | 82 | 0.00 | 17004.08 |
| yr + liveBA(T ₂₀) | yr + liveBA | 15.43 | 83 | 0.00 | 17003.63 |
| yr + snag | yr | 15.48 | 82 | 0.00 | 17005.82 |
| yr + snag ² | yr + liveBA | 15.69 | 83 | 0.00 | 17003.89 |

| | | | | | |
|-------------------------------|-------------------|--------------|-----------|-------------|-----------------|
| yr + liveBA(T ₂₀) | yr | 17.67 | 82 | 0.00 | 17008.01 |
| yr + liveBA | yr | 18.30 | 82 | 0.00 | 17008.64 |
| yr | yr + canopy cover | 18.33 | 82 | 0.00 | 17008.67 |
| yr + liveBA(T ₄₀) | yr | 18.34 | 82 | 0.00 | 17008.68 |
| yr + canopy cover | yr | 18.35 | 82 | 0.00 | 17008.69 |
| <u>yr</u> | <u>yr + snag</u> | <u>18.40</u> | <u>82</u> | <u>0.00</u> | <u>17008.73</u> |

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691 ^a yr = year-specific variation; snag = total (all tree species) density of snags ≥ 20 cm dbh and 1.8 m tall; liveBA = total (all tree species)

692 amount of live basal area (expressed as m² per 0.04 ha); (T_i) = minimum threshold values for the preceding habitat covariate.

693 ^b Minimum AIC_c = 17159.92

694 Figure 1. Boundaries (thick dashed line) for control (East Fork) and treatment (Coon Creek)
695 watersheds of the Sierra Madre Range in south-central Wyoming, USA. The thin dashed line
696 delineates the portion of Coon Creek that was used to evaluate squirrel responses to the patch-
697 cutting treatment. Gray areas indicate patch cuts and roads. Patch cuts were harvested August
698 1990-October 1992. Black dots represent location of sampling points ($n = 180$).

699
700 Figure 2. Changes in live basal area for lodgepole pine (*Pinus contorta*), Engelmann spruce
701 (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) combined at two watersheds of the
702 Sierra Madre Range in south-central Wyoming, USA. Vegetation surveys were conducted in
703 both control and treatment watersheds before (pre-harvest: 1985) and after patch-cutting (post-
704 harvest: 1992) occurred in the treatment watershed, and after broad-scale outbreaks of multiple
705 species of bark beetle in the Rocky Mountains (post-outbreak: 2011). Sampling points in the
706 treatment watershed that fell between patch cuts are labeled as “treatment uncut”, and points that
707 fell within 15 m of a patch cut are labeled as “treatment cut”.

708
709 Figure 3. Detection probabilities (p) by year and treatment for red squirrels at two watersheds in
710 south-central Wyoming, USA. Probability of detection was estimated for both watersheds before
711 (pre-harvest) and after (post-harvest) patch-cutting occurred in the treatment watershed, and after
712 a broad-scale bark beetle outbreak (post-outbreak) affected both watersheds. Detection
713 probabilities were estimated from the best-fit detection probability model using encounter
714 histories at 90 sampling points in each watershed. Sampling points in the treatment watershed
715 either fell within a cut (treatment cut) or between cuts (treatment uncut).

716

717 Figure 4. Mean probability of local extinction (ϵ) of red squirrels as a function of snag density
718 during 1985-1996 (before a bark beetle outbreak) and 2011-2012 (after the bark beetle outbreak)
719 at 90 sampling points in each of two watersheds of the Sierra Madre Range, south-central
720 Wyoming, USA. Snag density at the study site ranged from 0-11 snags/0.04 ha before the
721 outbreak and from 0-23 snags/0.04 ha after the outbreak. Estimates were generated from the best
722 model [$\psi(\cdot)$, $\epsilon(\text{yr} + \text{snagT}_5)$, $\gamma(\text{yr} + \text{liveBA})$, $p(\text{trt} \times \text{yr})$]. See Tables 2 and 3 for abbreviations.

723
724 Figure 5. Mean probability of local colonization (γ) of red squirrels as a function of total
725 (lodgepole pine + Engelmann spruce + subalpine fir) live basal area during 1985-1996 (before a
726 bark beetle outbreak) and 2011-2012 (after the bark beetle outbreak) at 90 sampling points in
727 each of two watersheds of the Sierra Madre Range, south-central Wyoming, USA. Total live
728 basal area at the study site ranged from 0-79 m²/0.04 ha before the outbreak and from 0-27
729 m²/0.04 ha after the outbreak. Estimates were generated from the best model [$\psi(\cdot)$, $\epsilon(\text{yr} +$
730 $\text{snagT}_5)$, $\gamma(\text{yr} + \text{liveBA})$, $p(\text{trt} \times \text{yr})$]. See Tables 2 and 3 for abbreviations.

731
732 Figure 6. Estimates of mean annual site occupancy of red squirrels at 180 sampling points in two
733 watersheds of the Sierra Madre Range, south-central Wyoming, USA before (pre-harvest) and
734 after (post-harvest) patch-cutting in the treatment watershed, and after a broad-scale bark beetle
735 outbreak (post-outbreak) in treatment and control watersheds. Estimates incorporate habitat
736 characteristics specific to each sampling point using initial occupancy, extinction, and
737 colonization probabilities from the best model [$\psi(\cdot)$, $\epsilon(\text{yr} + \text{snagT}_5)$, $\gamma(\text{yr} + \text{liveBA})$, $p(\text{trt} \times \text{yr})$].
738 See Tables 2 and 3 for abbreviations.

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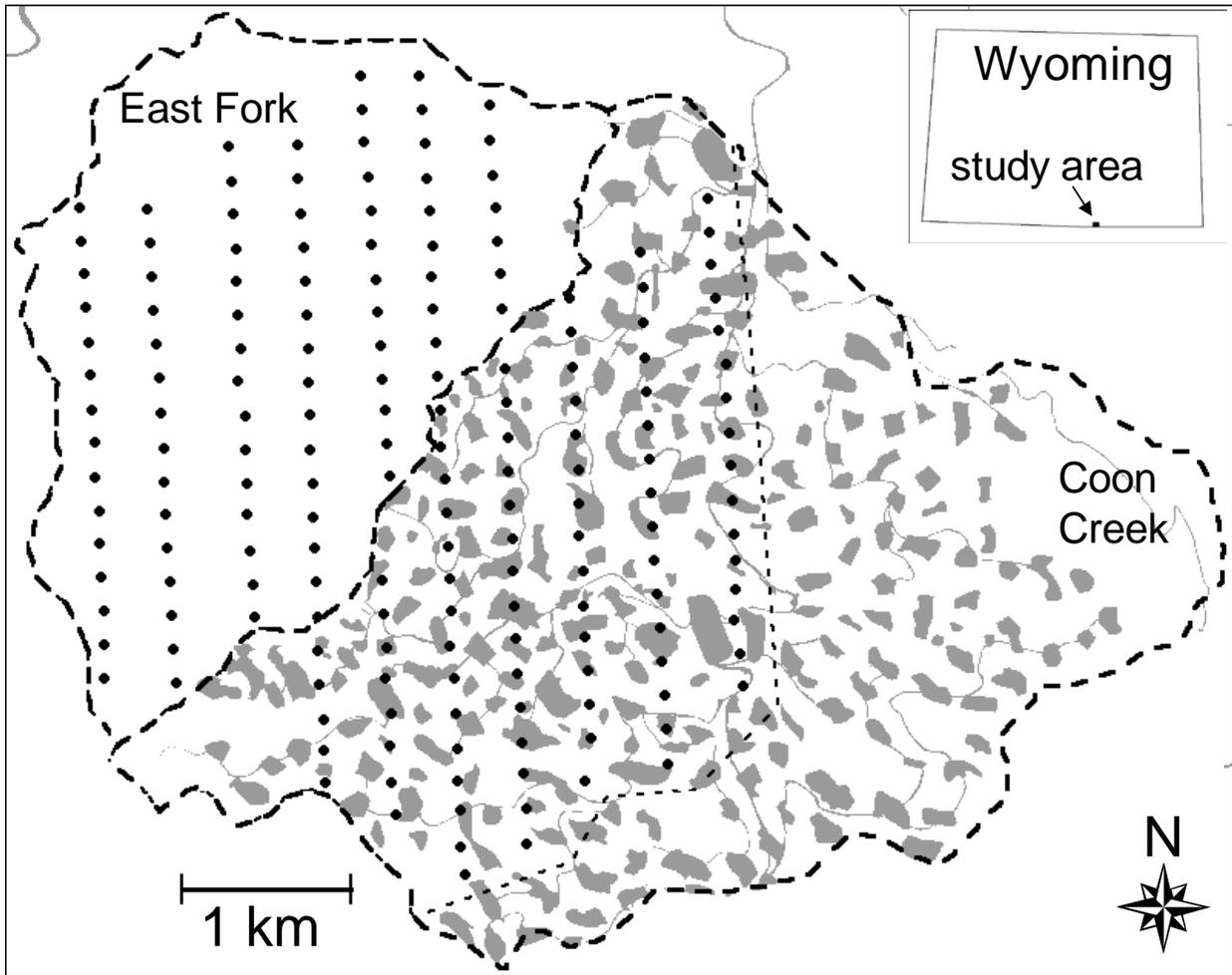
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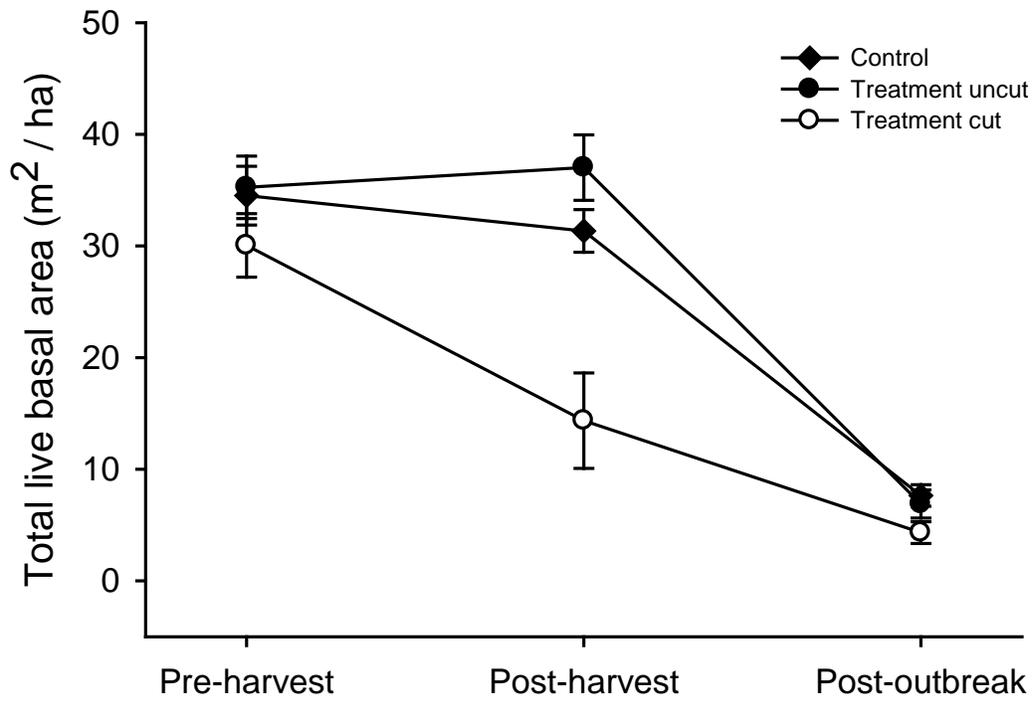
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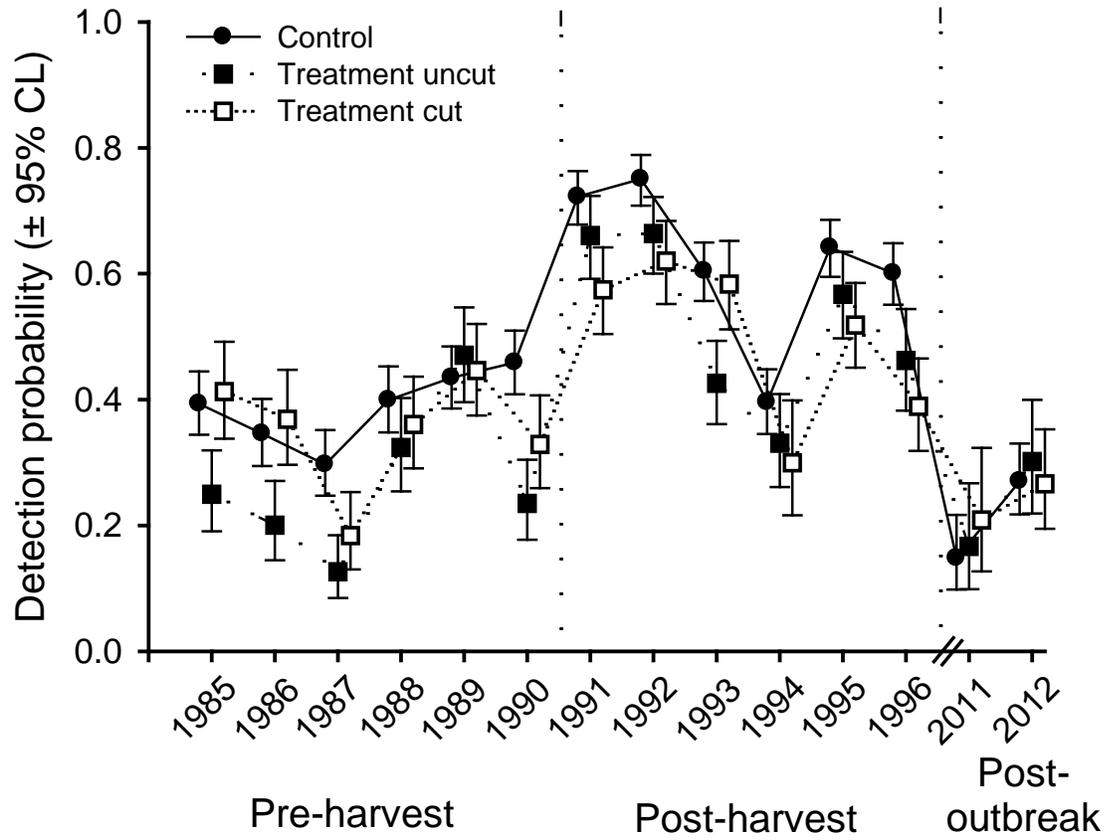
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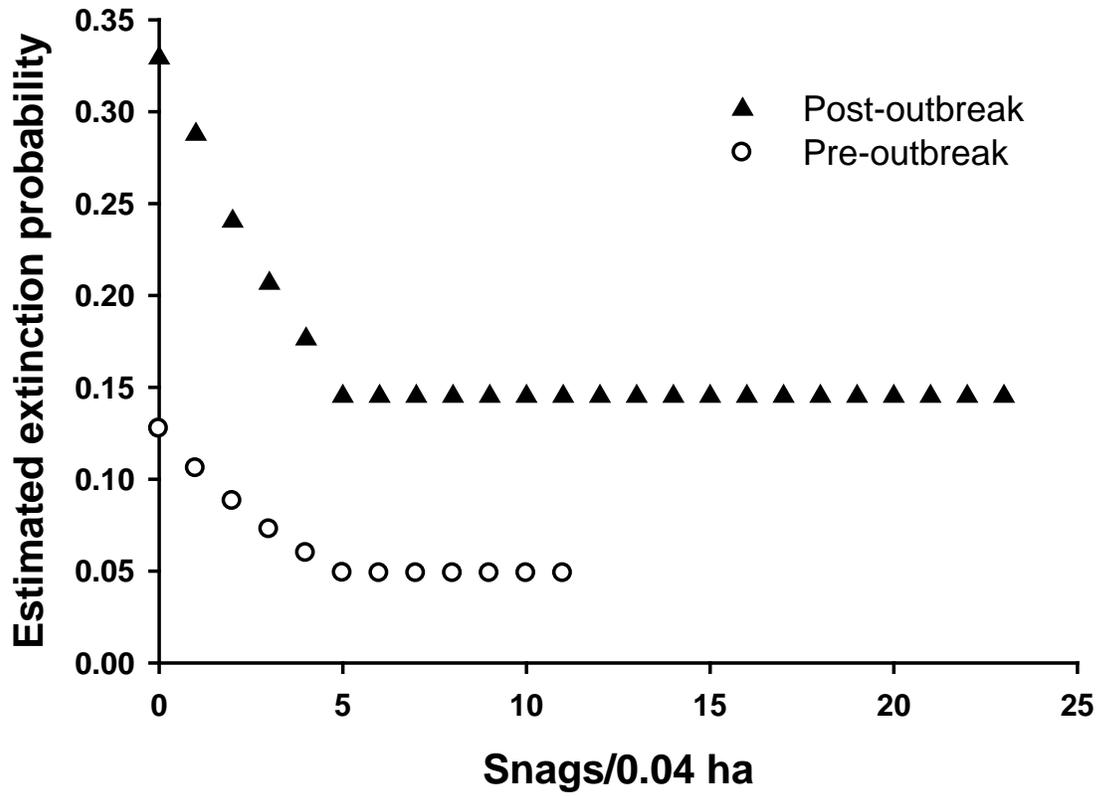
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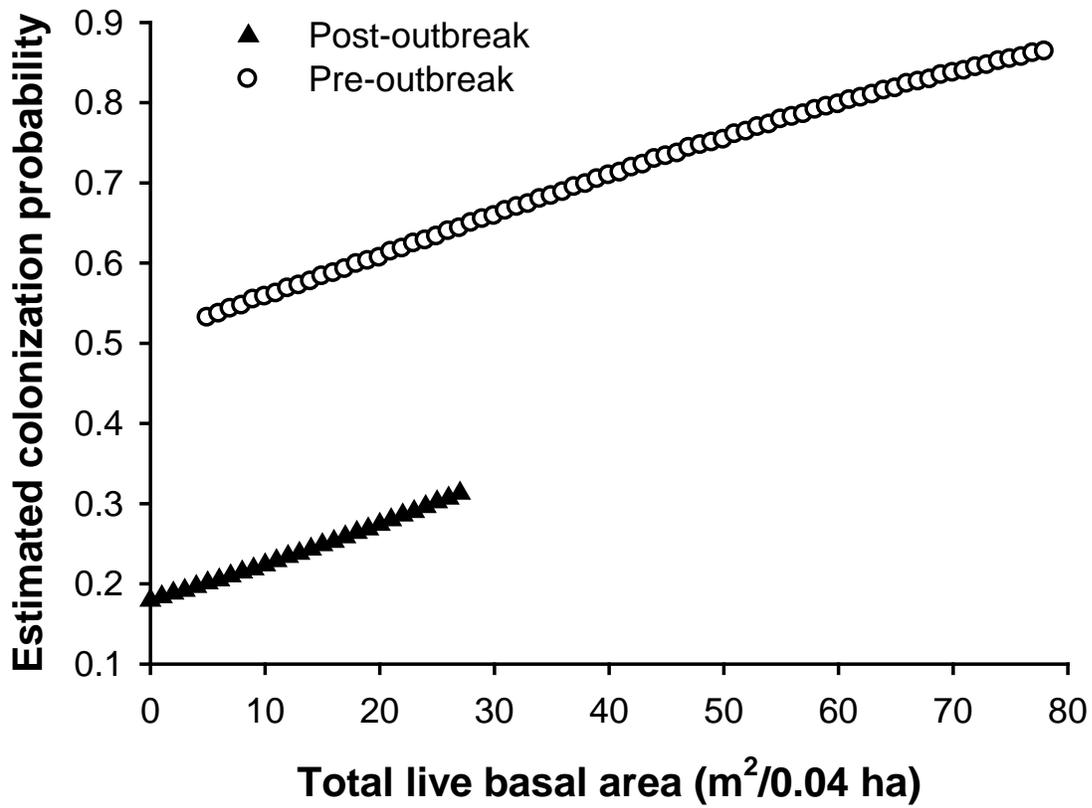
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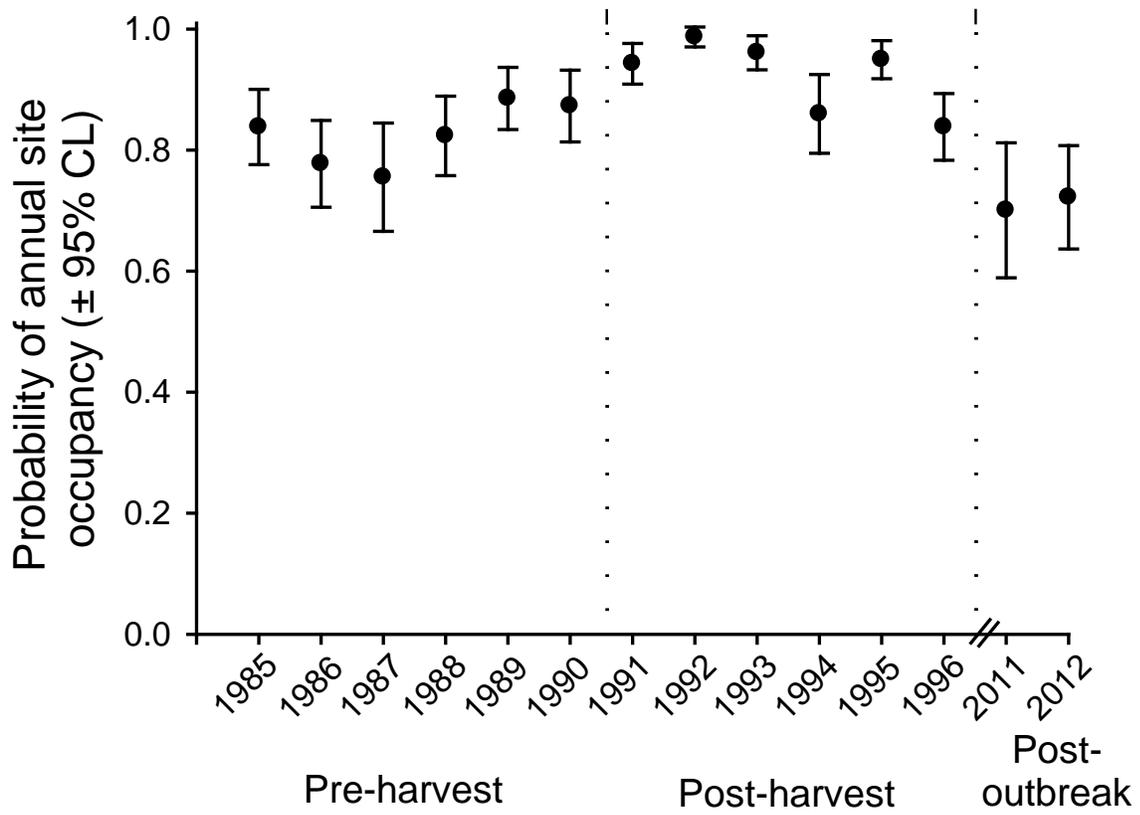
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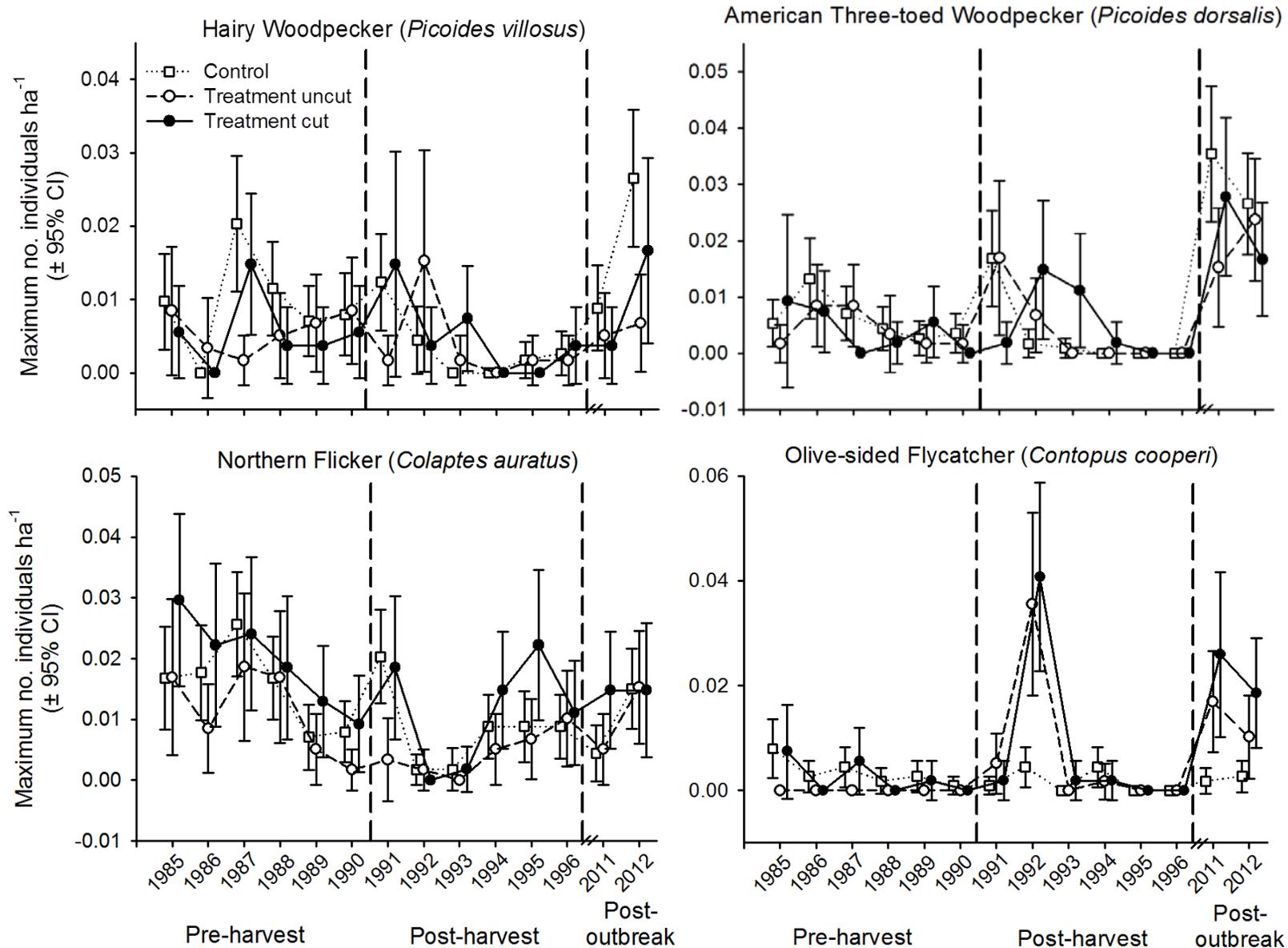
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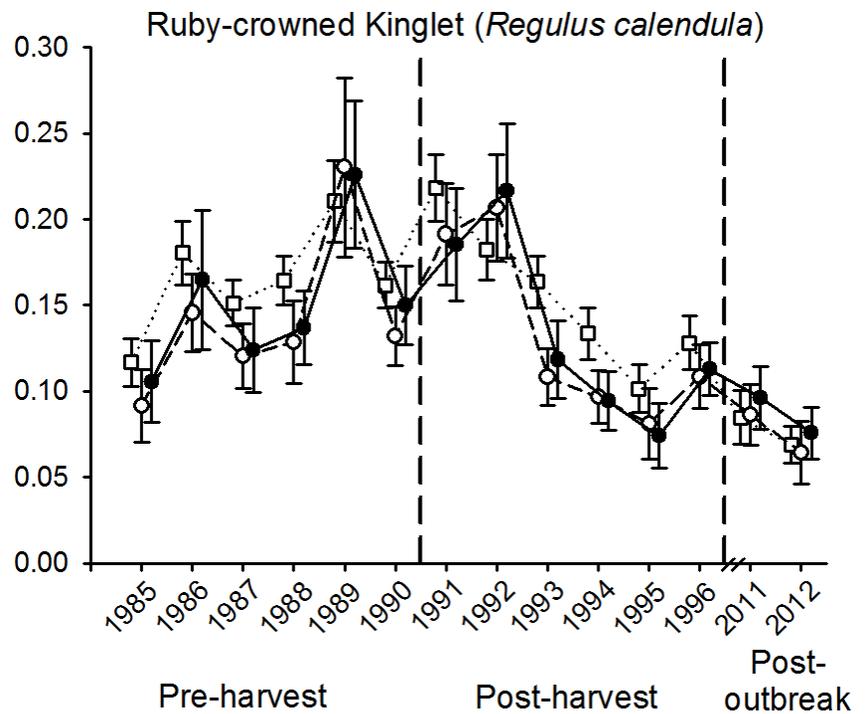
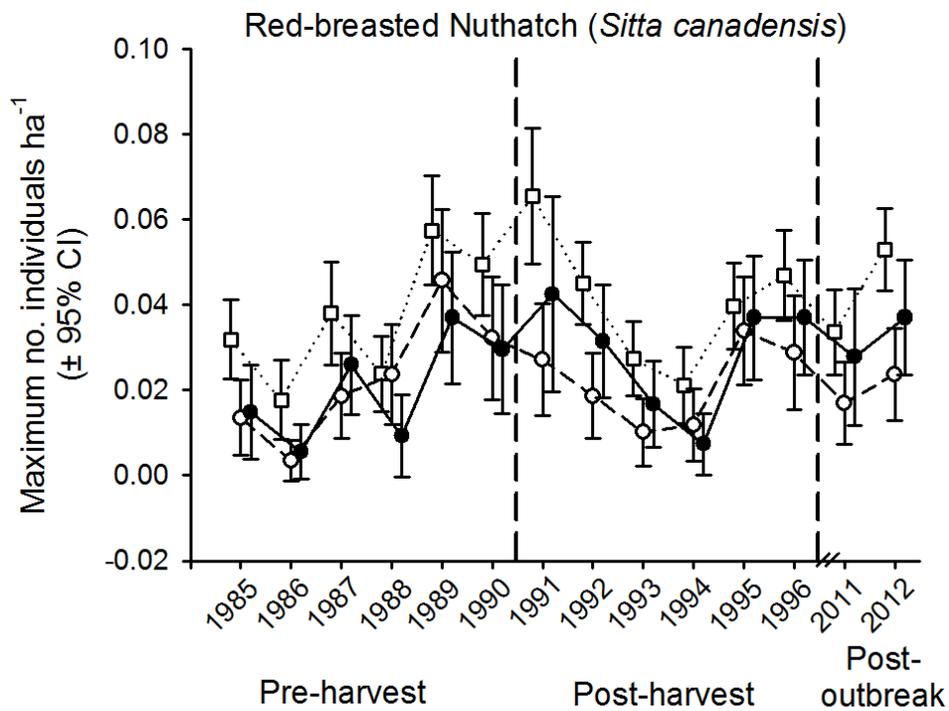
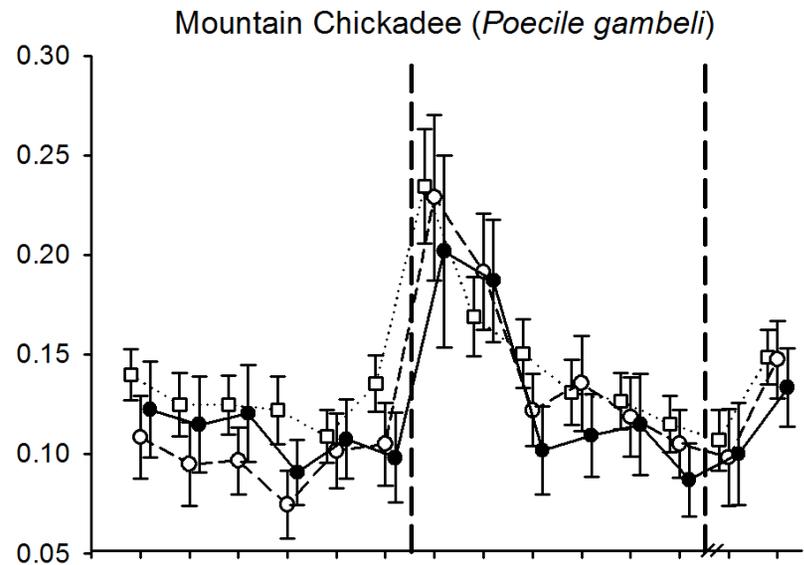
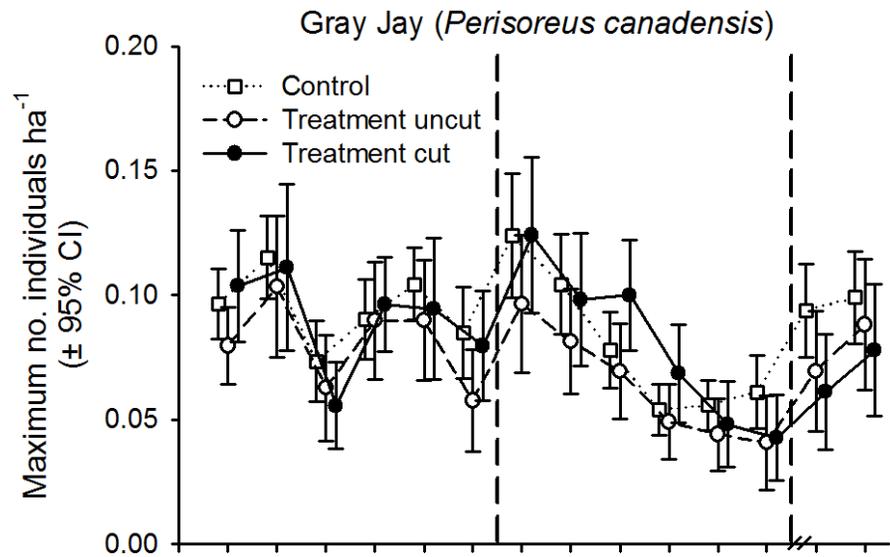


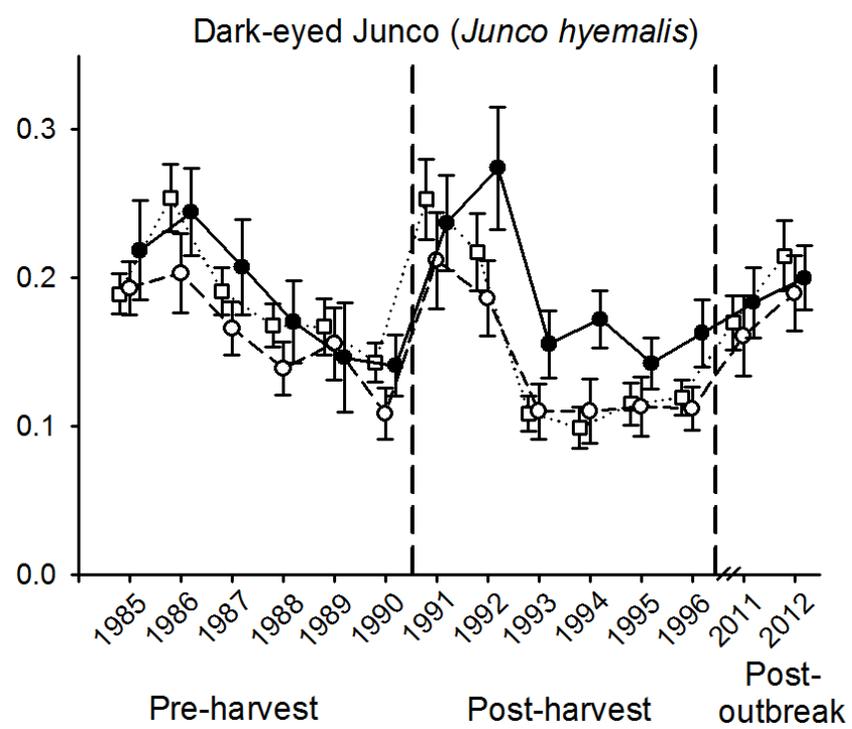
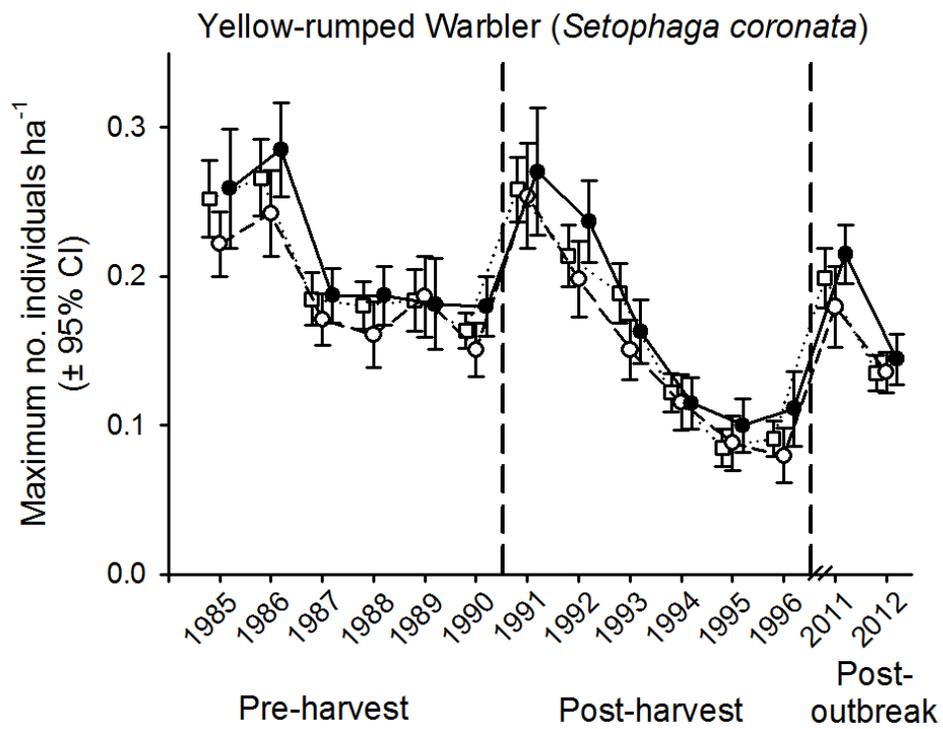
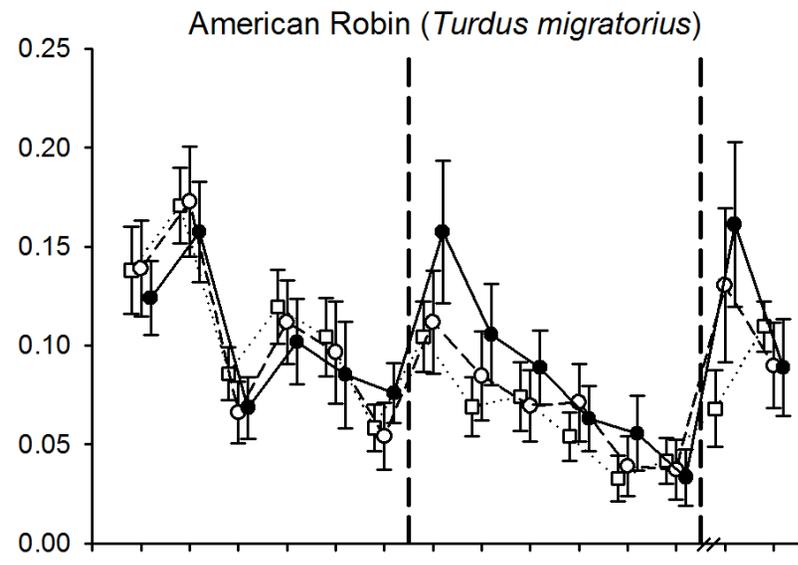
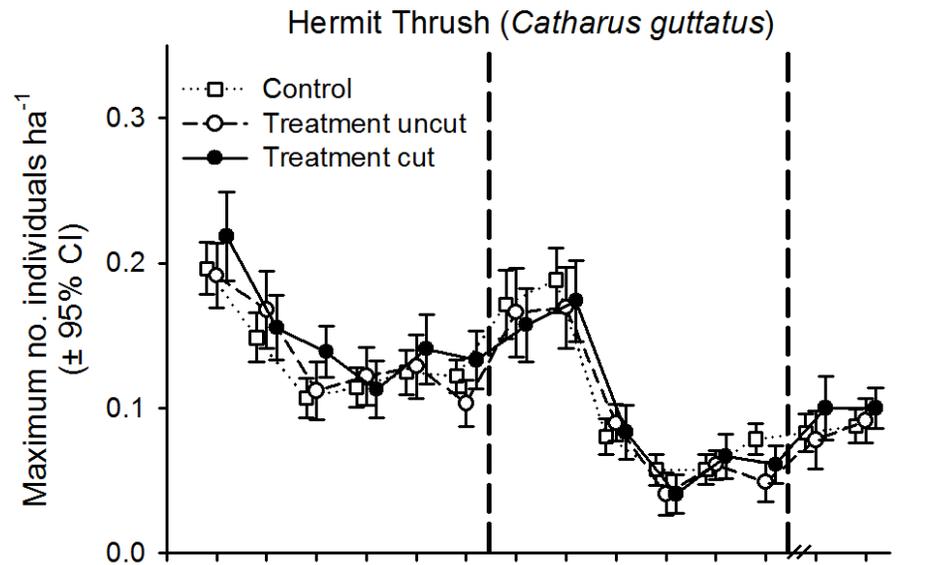
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884
885

Figure 6.

Fig. 1. Average (among all sampling points in each respective treatment category) of the maximum number of birds detected during 5-6 visits annually to each sampling point in two watersheds (control: East Fork; treatment: Coon Creek) in the Sierra Madre Range, south-central Wyoming. Point counts were conducted at 90 permanent sampling points in each watershed (treatment uncut: $n = 47$; treatment cut: $n = 43$). Harvesting occurred during 1990-92.







Pine Siskin (*Spinus pinus*)

