forest ecology

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., \leq 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

F orest 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 wood-peckers. 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 postoutbreak 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 assemblagelevel 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 largescale (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 (>6years 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 Douglasfir, 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 [Picoides villosus], and downy woodpecker [Picoides 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 specieslevel 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 \pm 0.4 m²/ha (mean \pm SE)] versus East Fork [7.7 \pm 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 Heyward (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 MKNA 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 cavitynesting 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.

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 | М | 2006-2009 | Not reported | Spatial |
| 8 | Drever and Martin (2007) ^{MPB,A,M} | BC | Peaked 2003 | М | 1995-2004 | 8.5×10^{6} | Temporal |
| 9 | Drever and Martin (2010) ^{PR,MPB,S,A} | BC | Peaked 2003 | М | 1997-2008 | $\geq 10^7$ | Temporal and spatial |
| 10 | Edworthy et al. (2010) ^{PR,MPB,S,A} | BC | Peaked 2003 | М | 1995-2009 | $\geq 10^7$ | 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 | М | 1996-1998 | 250,000 | Spatial |
| 13 | Martin and Norris (2007) ^{MPB,A} | BC | Peaked 2003 | М | 1995-2004 | $\geq 10^7$ | Spatial |
| 14 | Martin et al. (2006) ^{PR,MPB,A} | BC | Peaked 2003 | М | 1995-2005 | $\geq 10^7$ | 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 | М | 1995-2005 | $\geq 10^7$ | Spatial |
| 18 | Norris and Martin (2010) ^{PR,MPB,A} | BC | Peaked 2003 | М | 1997-2006 | $\geq 10^7$ | Temporal and spatial |
| 19 | Norris & Martin (2013) ^{PR,MPB,A} | BC | Peaked 2003 | М | 1997-2006 | $\geq 10^7$ | 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 | М | 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.

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.

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 water-thrush (*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

| Table 3. | Avian relationship | os with MPB | outbreaks reported | l in | reviewed stu | dies. |
|----------|--------------------|-------------|--------------------|------|--------------|-------|
| | | | | | | |

| Species (taxonomic name; assemblage: foraging, nest layer, nest type) | Ref. | No. sites | n | Response type | Response |
|--|--------|------------------|--------------------|--|--------------------|
| Bufflehead (<i>Bucephala albeola</i> ; OM, | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Sharp-shinned hawk (<i>Accipiter striatus</i> ; | 8 | 16 | 4,458 point-visits | Relative abundance $^{\mathrm{T}}$ | NS |
| Cooper's hawk (<i>Accipiter cooperii</i> ; CA, CA, O) | 8 | 16 | 4,458 point-visits | $Relative\ abundance^T$ | NS |
| Northern goshawk (Accipiter gentilis; | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| CA, CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Red-tailed hawk (Buteo jamaicensis; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| CA, CA, O) | 15 | 4 | 80 points | Occupancy ¹ | NS |
| American kestrel (<i>Falco sparverius</i> ; CA, CA, Cs) | 8 | 16 | 4,458 point-visits | Relative abundance ' | NS |
| Dusky grouse (<i>Dendragapus obscurus</i> ; OM, GR, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Ruffed grouse (Bonasa umbellus; OM, | 3 | 4^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| | 15 | 4 | 80 points | Occupancy ¹ | NS |
| Mourning dove (<i>Zenaida macroura</i> ; OM, SH, O) | 15 | 4 | 80 points | Occupancy ¹ | NS |
| Barred owl (Strix varia; 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 ¹ | NS |
| Great-horned owl (Bubo virginianus; | 3 | 4^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| CA, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Northern saw-whet owl (Aegolius | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| acadicus; CA, CA, Cs) | | | | T | |
| Common nighthawk (<i>Chordeiles</i> <i>minor</i> ; AI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ' | NS |
| Rufous hummingbird (<i>Selasphorus rufus</i> ; NE, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance $^{\mathrm{T}}$ | NS |
| American three-toed woodpecker | 3 | 4 ^{C1} | 48 points | Relative abundance ^S | None ^{NP} |
| (Picoides dorsalis; BD, CA, Cp) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ^T | + |
| | 9 | 23 | 242 point-years | Relative abundance ⁵ | + |
| | 10 | 20 | 317 nests | No. eggs/nestlings per nest | None |
| | 14 | 27 | Not recorded | Nest density | + |
| | 15 | 4 | 33 pests | Next density ^{T} | + |
| | 20 | 4 | 33 nests | Nest survival ^T | NS |
| Black-backed woodpecker (Picoides | 1 | ≥52 | 43 nests | Nest survival ^S | NS |
| arcticus; BD, CA, Cp) | 2 | ≥52 | 42 nests | Nest site selection ^S | 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 | NS |
| | 9 | 23 | 242 point-years | Relative abundance ^S | NS |
| Downy woodpecker (<i>Picoides</i> | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| <i>pubescens</i> ; BD, CA, Cp) | 9 | 23 | 242 point-years | Relative abundance | + |
| | 10 | 23 | 242 point-years | No eggs/pestlings per pest ^T | + NS |
| | 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 | + |
| Hairy woodpecker (<i>Picoides villosus</i> ; | 3 | 401 | 48 points | Relative abundance ^{3, w} | +"" |
| BD, CA, Cp) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 2 Q | ∠ <i>⊃</i> 23 | 242 point-years | Relative abundance ^S | + |
| | 10 | 20 | 68 nests | No. eggs/nestlings per nest ^T | NS |
| | 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 |
| Northern flicker (Colaptes auratus; | 3 | 4^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| OM, CA, Cp) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| | 9 | 23 | 242 point-years | Relative abundance ¹ | + |
| | 9 | 23 | 242 point-years | Relative abundance ⁵ | NS |
| | 10 | 20 | 31/ nests | No. eggs/nestlings per nest $\Omega_{\text{nestrong}} = T$ | NS |
| | 15 | 4 | 80 points | Next density ^T | INS NIC |
| | 20 | 4 | 27 110515 | inest delisity | 1NO |

(continued)

Table 3. (Continued.)

| Species (taxonomic name; assemblage: | | No. | | | |
|---|------|-----------------|---------------------------|--|--------------------------|
| foraging, nest layer, nest type) | Ref. | sites | n | Response type | Response |
| Northern flicker (Colaptes auratus; | 20 | 4 | 27 nests | Nest survival ^T | NS |
| OM, CA, Cp) | 22 | 40 | 160 points | Relative density ^S | NS |
| Pileated woodpecker (Dryocopus | 3 | 4^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| pileatus; OM, CA, Cp) | 4 | 7 ^{IS} | Not recorded for density; | density and reproductive success $^{\mathrm{T}}$ | NS ^{C2} |
| | | | 11 pairs for | | |
| | | | reproductive success | _ | |
| | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 9 | 23 | 242 point-years | Relative abundance ¹ | + |
| | 9 | 23 | 242 point-years | Relative abundance ³ | + |
| | 14 | 27 | Not recorded | Nest density | NSIN |
| | 15 | 4 | 80 points | Occupancy ¹ | NS |
| Red-naped sapsucker (Sphyrapicus | 8 | 16 | 4,458 point-visits | Relative abundance | |
| nuchaus; OM, CA, Cp) | 9 | 23 | 242 point-years | Relative abundance | INS NS |
| | 10 | 23 | 242 point-years | No. $eggs/pectlings per pectT$ | NS |
| | 10 | 20 | 80 points | $\Omega_{\rm ccupapev}^{\rm T}$ | NS |
| | 20 | 4 | 95 nests | Nest density ^T | NS |
| | 20 | 4 | 95 nests | Nest survival ^T | NS |
| White-headed woodpecker (Picaides | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| albolarvatus; OM, CA, Cp) | - | | I | | |
| Alder flycatcher (Empidonax alnorum; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| AI, SH, O) | | | 1 | | |
| Dusky flycatcher (Emidonax | 15 | 4 | 80 points | Occupancy ^T | + |
| oberholseri; AI, SH, O) | | | * | | |
| Hammond's flycatcher (Empidonax | 15 | 4 | 80 points | Occupancy ^T | + |
| hammondii; AI, CA, O) | | | | | |
| Least flycatcher (Empidonax minimus; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| AI, SH, O) | | | | | |
| Olive-sided flycatcher (Contopus | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| cooperi; AI, CA, O) | 22 | 40 | 160 points | Relative density ^S | + |
| Pacific-slope flycatcher (Empidonax | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | NS |
| difficilis; AI, CA, Cs) | | | | | |
| Western wood peewee (Contopus | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | - |
| sordidulus; AI, CA, O) | 0 | 16 | ((50 | | |
| Willow flycatcher (<i>Empidonax traillii</i> ; | 8 | 16 | 4,458 point-visits | Relative abundance ² | + |
| AI, SH, O) Tree multiple (Technicity to bischer AI | 0 | 16 | 4 450 | Delection along of T | NIC |
| Tree swallow (<i>Tacnycineta bicolor</i> ; Al, | 0 | 16 | 4,438 point-visits | | INS NS |
| Violet green swallow (Tachwinata | 1) | 4 | 4 458 point visite | Relative abundance ^T | NS |
| thalassina: AL CA Cs) | 0 | 10 | 4,496 point-visits | Relative abundance | 143 |
| American crow (Corvus | 8 | 16 | 4.458 point-visits | Relative abundance ^T | NS |
| brachvrhvnchos: OM, CA, O) | 0 | 10 | 1,190 point (1010) | Telative abundance | 110 |
| Black-billed magpie (<i>Pica hudsonia</i> ; | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Clark's nutcracker (Nucifraga | 15 | 4 | 80 points | Occupancy ^T | NS |
| columbiana; PSC, CA, O) | | | * | | |
| Common raven (Corvus corax; OM, | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Gray jay (Perisoreus canadensis; OM, | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| CA, O) | 6 | 21 | 116 points | Relative abundance ^S | + ^{NP} |
| | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | NS |
| | 15 | 4 | 80 points | Occupancy ¹ | NS |
| | 22 | 40 | 160 points | Relative density ³ | NS |
| Steller's jay (<i>Cyanocitta stelleri</i> ; OM, | 3 | 401 | 48 points | Relative abundance ^{3, w} | NST |
| CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Black-capped chickadee (Poecile | 8 | 16 | 4,458 point-visits | Kelative abundance | INS NIC ^{NP} |
| atricapulus; F1, CA, CS) | 14 | 2/ | Not recorded | | 185 |
| Borreal chickades (Passile hudsonicus | 1) | 4 | 4 458 point visite | Relative abundance ^T | + |
| FL CA C) | 0 | 10 | 4,456 point-visits | Relative abundance | 1 |
| Mountain chickadee (Poecile aambeli: | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | _NP |
| FI, CA, Cs) | 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 (Certhia americana; | 3 | 4^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| BG, CA, Cs) | 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 |

Table 3. (Continued.)

| Species (taxonomic name; assemblage: | | No. | | | |
|--|------|-----------------|-------------------------|-------------------------------------|-----------------------|
| foraging, nest layer, nest type) | Ref. | sites | 2 | Response type | Response |
| Red-breasted nuthatch (Sitta | 3 | 4^{C1} | 48 points | Relative abundance ^{S,W} | _NP |
| canadensis: BG, CA, Cp) | 8 | 16 | 4.458 point-visits | Relative abundance ^T | NS |
| | 14 | 27 | Not recorded | Nest density ^T | Mixed ^{NP,C} |
| | 15 | 4 | 80 | Occupancy ^T | NS |
| | 17 | 27 | 231 nests: 1,136 random | Nest site selection ^S | + |
| | - / | _, | points | | |
| | 18 | 27 | 425 points | Relative density ^B | + C6 |
| | 22 | 40 | 160 points | Relative density ^S | + |
| White-breasted nutbatch (Sitta | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NSNP |
| carolinensis BC CA Cs) | 15 | 4 | 80 points | | NS |
| House wren (Tradadutes adam: CI | 15 | 4 | 80 points | Occupancy ^T | + |
| CA Cs) | 1) | 4 | so points | Occupancy | 1 |
| Winter wron (Tradadute hier din CI | 6 | 21 | 116 points | Polativo abundan ao ^S | minodNP |
| white wien (<i>Trogiouyies memuus</i> ; Gi, | 0 | 21 | 4 450 mainterrivity | Deleving abundance | NIC |
| Calden and him lat (Damilia | 0 | 4C1 | 4,458 point-visits | Deleving abundance | INS NP |
| Golden-crowned kinglet (<i>Regulus</i> | 3 | 4 | 48 points | Relative abundance | - NP |
| satrapa; FI, CA, O) | 6 | 21 | 116 points | Relative abundance [®] | + |
| | 8 | 16 | 4,458 point-visits | Relative abundance | - |
| Ruby-crowned kinglet (Regulus | 6 | 21 | 116 points | Relative abundance ³ | NS ^{INF} |
| calendula; FI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | + |
| | 14 | 27 | Not recorded | Nest density ¹ | NS ^{NP} |
| | 15 | 4 | 80 points | Occupancy ¹ | + |
| American robin (Turdus migratorius; | 6 | 21 | 116 points | Relative abundance ^S | $+^{NP}$ |
| GI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Hermit thrush (Catharus guttatus; GI, | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| SH, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Mountain bluebird (Sialia currucoides; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| AL CA, Cs) | 15 | 4 | 80 points | Occupancy ^T | + |
| 11, 61, 65) | 22 | 40 | 160 points | Relative density ^S | + |
| Swainson's thrush (Catharus ustulatus | 6 | 21 | 116 points | Relative abundance ^S | _NP |
| FL SH () | 8 | 16 | 4 458 point vicits | Relative abundance ^T | + |
| 11, 511, 0) | 15 | 10 | 90 points | | - - |
| | 13 | 4 | 80 points | DL | Ŧ |
| I ownsend s solitaire (<i>Myadestes</i> | 0 | 16 | 4,438 point-visits | | — NIC |
| townsenat; AI, GK, O) | 15 | 4 | 80 points | Occupancy | INS |
| Varied thrush (Ixoreus naevius; GI, | 8 | 16 | 4,458 point-visits | Relative abundance ² | - |
| CA, O) | | | | · · · · · · · · · · · · · · · · · · | |
| Veery (Catharus fuscescens; GI, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | NS |
| European starling (Sturnus vulgaris; | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | - |
| GI, CA, Cs) | | | | | |
| Bohemian waxwing (Bombycilla | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| garrulus; OM, CA, O) | | | | | |
| Cedar waxwing (Bombycilla cedrorum; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| OM, CA, O) | | | • | | |
| Cassin's vireo (Vireo cassinii; FI, | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Warbling vireo (Vireo gilvus: FL 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 workler (Sataphaga striata | 8 | 16 | 4 458 point vicits | Relative shundance ^T | NS |
| BC SH () | 0 | 10 | 4,490 point-visits | Relative abundance | 145 |
| Marcillianers's model on (Contribution | 0 | 16 | 6 650 | Delection about dam of T | |
| MacGillivray's warbler (<i>Geotnlypis</i> | 8 | 16 | 4,458 point-visits | | _ |
| tolmiet; FI, SH, O) | 15 | 4 | 80 points | Occupancy | + |
| Magnolia warbler (Setophaga magnolia; | 8 | 16 | 4,458 point-visits | Relative abundance ² | NS |
| FI, CA, O) | | | | · · · · · · · · · · · · · · · · · · | |
| Northern waterthrush (Parkesia | 8 | 16 | 4,458 point-visits | Relative abundance ¹ | NS |
| noveboracensis; GI, GR, O) | | | | | |
| Orange-crowned warbler (Oreothlypis | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| celata; FI, GR, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| Townsend's warbler (Setophaga | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | NS ^{NP} |
| townsendi; FI, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| Wilson's warbler (Cardellina pusilla; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| FI, GR, O) | | | * | | |
| Yellow warbler (Setophaga petechia: FI | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| SH. O) | 0 | | 1, 190 Point Visito | relative abundance | |
| Vallow rumped workler (Setechard | 6 | 21 | 116 points | Pelative abundance ^S | NICNP |
| renow-rumped wardier (Setophaga | 0 | 21 | 4 6 9 m - int | Relative abundance | 1N5 |
| coronata; FI, CA, U) | 8 | 16 | 4,458 point-visits | Kelative abundance ⁻ | - |
| | 15 | 4 | 80 points | Occupancy ⁴ | NS |
| | 22 | 40 | 160 points | Relative density ⁵ | NS |
| Chipping sparrow (Spizella passerina; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 6 | 20 mainte | Occupancy ^T | + |
| OM, SH, O) | 15 | 4 | 80 points | Occupancy | |

(continued)

Table 3. (Continued.)

| Species (taxonomic name; assemblage: | | No. | | | |
|--|------|-----------------|--------------------|-----------------------------------|-----------------|
| foraging, nest layer, nest type) | Ref. | sites | n | Response type | Response |
| Dark-eved junco (Junco hyemalis; OM, | 6 | 21 | 116 points | Relative abundance ^S | _NP |
| GR, O) | 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 (Melospiza lincolnii; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| OM, GR, O) | 15 | 4 | 80 points | Occupancy ^T | + |
| Savannah sparrow (<i>Passerculus</i> sandwichensis; 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 (Pooecetes gramineus; | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| OM, GR, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| White-crowned sparrow (<i>Zonotrichia</i> <i>leucophrys</i> ; OM, GR, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Black-headed grosbeak (<i>Pheucticus</i> melanocephalus; 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</i> <i>cyanocephalus</i> ; OM, SH, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | - |
| Brown-headed cowbird (Molothrus | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| <i>ater</i> ; OM, -, P) | 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 (Piranga ludoviciana; | 6 | 21 | 116 points | Relative abundance ^S | - ^{NP} |
| FI, 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 | + |
| Pine grosbeak (<i>Pinicola enucleator</i> ; PSC, CA, O) | 22 | 40 | 160 points | Relative density ^S | NS |
| Cassin's finch (Haemorhous cassinii; | 3 | 4 ^{C1} | 48 points | Relative abundance ^{S,W} | $+^{NP}$ |
| OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Pine siskin (Spinus pinus; OM, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| | 15 | 4 | 80 points | Occupancy ^T | + |
| Red crossbill (Loxia curvirostra; PSC, | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| CA, O) | 15 | 4 | 80 points | Occupancy ^T | NS |
| White-winged crossbill (<i>Loxia</i> <i>leucoptera</i> ; PSC, CA, O) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | NS |
| Evening grosbeak (Coccothraustes | 8 | 16 | 4,458 point-visits | Relative abundance ^T | + |
| vespertinus; OM, CA, O) | 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.

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, 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.



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.

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 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 preoutbreak 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 peerreviewed. 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 snow-shoe 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 m²/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-m² increase in

| Tab | e 4. | Mammalian | relationsh | ips wit | h MPB | outbreak | cs as re | eported | in artic | les reviewed |
|-----|------|-----------|------------|---------|-------|----------|----------|---------|----------|--------------|
| | | | | | | | | | | |

| Species (taxonomic name) | Ref. | No. sites | Ν | Response type | Response |
|--|------|-----------|-------------------------------------|--------------------------------------|--------------------------|
| Snowshoe hare (Lepus americanus) | 22 | 40 | 50-10 m ² circular plots | Relative abundance ^S | Mixed ^{C1} |
| Chipmunk (Neotamias minimus and Neotamias umbrinus) | 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 (Tamiasciurus hudsonicus) | 8 | 16 | 4,458 point-visits | Relative abundance ^T | — |
| A · | 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 (Glaucomys sabrinus) | 22 | 40 | 8 transects | Relative abundance ^s | + ^{C3} |
| Deer mouse (Peromyscus maniculatus) | 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 (Cervus canadensis) | 22 | 40 | $50-10 \text{ m}^2$ circular plots | Relative abundance ^s | + ^{C3} |
| Mule deer (Odocoileus hemionus) | 22 | 40 | 50–10 m ² circular plots | Relative abundance ^s | + ^{C3} |
| Moose (Alces alces) | 22 | 40 | 50–10 m ² circular plots | Relative abundance ^S | + ^{C3} |
| Northern caribou (Rangifer tarandus) | 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 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.

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 m²/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 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 \pm 1.3) and percent dead spruce ranged from 0 to 60% (15.4 \pm 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

| Table 5. | Avian and | mammalian | relationships | with | salvaae | loaaina | after MP | B outbreak | s reported | in reviewed | articles. |
|----------|-----------|-----------|---------------|------|---------|---------|----------|------------|------------|-------------|-----------|
| | | | | | | | | | | | |

| Class | Species (taxonomic name) | Ref. | No. sites | n | Response type | Response |
|----------|--|------|---------------------|-------------------------|---|------------------------|
| Aves | American three-toed woodpecker (Picoides dorsalis) | 9 | 23 | 242 point-years | Count ^B | NS |
| | | 10 | 20 | 317 nests | No. eggs or nestlings per nest ^B | NS |
| | Black-backed woodpecker (Picoides arcticus) | 9 | 23 | 242 point-years | Count ^B | NS |
| | * | 12 | 24 | 193 points | Abundance ^S | NS ^{C1,C2} |
| | Downy woodpecker (Picoides pubescens) | 9 | 23 | 242 point-years | Count ^B | + |
| | | 10 | 20 | 91 nests | No. eggs or nestlings per nest ^B | NS |
| | Hairy woodpecker (Picoides villosus) | 9 | 23 | 242 point-years | Count ^B | $+^{C4}$ |
| | | 10 | 20 | 68 nests | No. eggs or nestlings per nest ^B | NS |
| | | 12 | 24 | 203 points | Abundance ^s | NS ^{C1,C2} |
| | Northern flicker (Colaptes auratus) | 9 | 23 | 242 point-years | Count ^B | $+^{C4}$ |
| | | 10 | 20 | 317 nests | No. eggs or nestlings per nest ^B | NS |
| | Pileated woodpecker (Dryocopus pileatus) | 9 | 23 | 242 point-years | Count ^B | $+^{C4}$ |
| | | 10 | 20 | 29 nests | No. eggs or nestlings per nest ^B | NS |
| | Red-naped sapsucker (Sphyrapicus nuchalis) | 9 | 23 | 242 point-years | Count ^B | + |
| | | 10 | 20 | 284 nests | No. eggs or nestlings per nest ^B | NS |
| | Dusky flycatcher (Empidonax oberholseri) | 12 | 24 | 199 points | Abundance ^s | NS ^{C1,C2} |
| | Gray flycatcher (Empidonax wrightii) | 12 | 24 | 200 points | Abundance ^S | NS ^{C1,C2,C3} |
| | Gray jay (Perisoreus canadensis) | 12 | 24 | 201 points | Abundance ^S | NS ^{C1,C2} |
| | Mountain chickadee (Poecile gambeli) | 12 | 24 | 206 points | Abundance ^S | NS ^{C1,C2} |
| | Brown creeper (Certhia americana) | 12 | 24 | 194 points | Abundance ^S | NS ^{C1,C2} |
| | Red-breasted nuthatch (Sitta canadensis) | 12 | 24 | 209 points | Abundance ^S | NS ^{C1,C2} |
| | White-breasted nuthatch (Sitta carolinensis) | 12 | 24 | 212 points | Abundance ^S | NS ^{C1,C2} |
| | American robin (Turdus migratorius) | 12 | 24 | 192 points | Abundance ^S | NS ^{C1,C2} |
| | Hermit thrush (Catharus guttatus) | 12 | 24 | 204 points | Abundance ^S | NS ^{C1,C2} |
| | Mountain bluebird (Sialia currucoides) | 12 | 24 | 205 points | Abundance ^S | NS ^{C1,C2} |
| | Townsend's solitaire (Myadestes townsendi) | 12 | 24 | 210 points | Abundance ^S | NS ^{C1,C2} |
| | Yellow-rumped warbler (Setophaga coronata) | 12 | 24 | 213 points | Abundance ^S | NS ^{C1,C2} |
| | Green-tailed towhee (Pipilo chlorurus) | 12 | 24 | 202 points | Abundance ^S | NS ^{C1,C2} |
| | Chipping sparrow (Spizella passerina) | 12 | 24 | 197 points | Abundance ^S | NS ^{C1,C2} |
| | Dark-eyed junco (Junco hyemalis) | 12 | 24 | 198 points | Abundance ^S | $+^{C1,C2}$ |
| | Brown-headed cowbird (Molothrus ater) | 12 | 24 | 195 points | Abundance ^S | NS ^{C1,C2} |
| | Western tanager (Piranga ludoviciana) | 12 | 24 | 211 points | Abundance ^S | NS ^{C1,C2} |
| | Cassin's finch (Haemorhous cassinii) | 12 | 24 | 196 points | Abundance ^S | $+^{C1,C2}$ |
| | Pine siskin (Spinus pinus) | 12 | 24 | 207 points | Abundance ^S | NS ^{C1,C2} |
| | Red crossbill (Loxia curvirostra) | 12 | 24 | 208 points | Abundance ^S | NS ^{C1,C2} |
| Mammalia | Common shrew (Sorex araneus) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | Montane shrew (Sorex monticolus) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | Northwestern chipmunk (Neotamias amoenus) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | Red squirrel (Tamiasciurus hudsonicus) | 23 | 12 | 1,200 trapping stations | Abundance ^B | NS ^{C5} |
| | Northern flying squirrel (Glaucomys sabrinus) | 23 | 12 | 1,200 trapping stations | Abundance ^B | NS |
| | Deer mouse (Peromyscus maniculatus) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | Southern red-backed vole (Clethrionomys gapperi) | 23 | 12 | 588 trapping stations | Abundance ^B | _C6 |
| | Heather vole (Phenacomys intermedius) | 23 | 12 | 588 trapping stations | Abundance ^B | + ^{C7} |
| | Long-tailed vole (Microtus longicaudus) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | Meadow vole (Microtus pennsylvanicus) | 23 | 12 | 588 trapping stations | Abundance ^B | NS |
| | Grizzly bear (Ursus arctos) | 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 (Rangifer tarandus) | 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 cublocks 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.

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, 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 singleseed 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 predictions. Cavity-nesting species responded more favorably to beetlekilled 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., rednaped 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 MPBaffected 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 smallscale 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 largescale 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 beetleinduced 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 responses 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 barkdrilling 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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