

Mammalian responses to changed forest conditions resulting from bark beetle outbreaks in the southern Rocky Mountains

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Abstract. Spruce beetle (*Dendroctonus rufipennis*) and mountain pine beetle (*Dendroctonus ponderosae*) outbreaks have impacted millions of acres of conifer forest from Alaska to northern Mexico. These species are native to North America, and periodic outbreaks have shaped the structure and composition of conifer forests for millennia. However, the extent and severity of current outbreaks, fueled by favorable climatic conditions and increased susceptibility of forests, are unmatched in recorded history. To characterize the response of a suite of mammalian species to beetle-induced changes in vegetation in the southern Rocky Mountains, we deployed cameras at 300 randomly selected sites during summer 2013–2014. Selected sites spanned gradients of years elapsed since bark beetle outbreaks (YSO) and severity. We fit single-season occupancy models to detection/non-detection data collected for each species to examine a variety of plausible relationships between use of a given stand and YSO, severity, or both. Ungulates exhibited a positive association with bark beetle activity, although the nature of these associations varied by species. Elk (*Cervus canadensis*) were positively associated with severity, but not YSO; mule deer (*Odocoileus hemionus*) exhibited the opposite relationship. Moose (*Alces alces*) responded in a quadratic fashion; use of forest stands adjacent to preferred willow habitat peaked 3–7 yr after an outbreak commenced, but only at high severity. Similarly, yellow-bellied marmot use of impacted stands adjacent to rock outcroppings followed a quadratic trend, but only at high severity. Red squirrel (*Tamiasciurus hudsonicus*) use declined in severely impacted stands, likely as a response to diminished cone crops. Golden-mantled ground squirrels (*Callospermophilus lateralis*) and chipmunks (*Neotamias* spp.) exhibited a shallow negative relationship with YSO, as did coyotes (*Canis latrans*). Contrary to our hypotheses, black bears (*Ursus americanus*), American marten (*Martes americana*), snowshoe hares (*Lepus americanus*), and porcupines (*Erethizon dorsatum*) did not appear to be substantially influenced by beetle activity. Red fox (*Vulpes vulpes*) use was positively associated with YSO, but overall use declined as severity increased. Note that changes in probability of use described here could reflect changes in abundance, home range size, habitat use, or some combination, and in several cases, there was considerable uncertainty across competing models.

Key words: bark beetle outbreak; camera trap; climate change; Colorado; *Dendroctonus ponderosae*; *Dendroctonus rufipennis*; mammals; mountain pine beetle; spruce beetle.

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INTRODUCTION

Native bark beetles are important disturbance agents in conifer forests of western North America. Along with fire, they have shaped forest composition and structure for millennia (Veblen 2000). While insect activity is a naturally occurring phenomenon in this region, the simultaneous eruptions of several species of bark beetle, and the extent and severity of these impacts (e.g., billions of trees situated on hundreds of millions of acres), are unmatched in recorded history (Bentz et al. 2009).

Generally, the life cycle of bark beetles proceeds as follows: Adults attack a specific species of live conifer tree, usually of larger diameter (e.g., >10 cm diameter at breast height), by burrowing through the bark and into the phloem. There, they copulate, excavate egg galleries, and deposit their eggs. When larvae hatch, they produce more galleries as they feed on phloem tissue. Eventually, larvae pupate and adults emerge from the tree, ready to attack again. The excavation of the egg galleries by the adult and feeding galleries by the larvae serves to interrupt the flow of water and nutrients within the tree resulting in its death (Raffa et al. 2008, Bentz et al. 2009, 2010).

This phenomenon has ecological consequences at multiple spatio-temporal scales. At the forest stand scale, beetle outbreaks and ensuing death of individual trees alter the age, size, and species composition of the stand. The death of individual trees also results in decreased canopy cover, changes in the understory due to increased sunlight, and accumulation of coarse wood. (Raffa et al. 2008, Bentz et al. 2009). The effects of these relatively sudden changes propagate through several decades as the stand is reverted to an earlier successional sere. At a larger scale, impacts caused by beetles at the stand level manifest as changed mosaics of stand types across the landscape, the signature of which may last a century or more (Raffa et al. 2008).

Lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*) forests are among the most common and expansive cover types in mountainous regions of western North America (Alexander and Shepperd 1990, Alexander et al. 1990, Lotan and Critchfield 1990). In recent decades, these forest

types have been heavily and extensively impacted by two species of bark beetle: mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*Dendroctonus rufipennis*), respectively. Two primary factors have propelled current outbreaks of these bark beetle species to epidemic levels. First, historical events have primed the susceptibility of these host forests to bark beetle outbreaks. That is, in many places forests are characterized by relatively dense, uniform stands of mature trees that are favored for successful completion of the bark beetle life cycle (Fettig et al. 2007, Raffa et al. 2008, Bentz et al. 2009). This has resulted largely from stand-replacing forest fires and extensive timber harvest near the turn of the 20th century (Fettig et al. 2007, Bentz et al. 2009).

Second, rising global temperatures have increased the vulnerability of host trees to infestation, while simultaneously enhancing the growth and development of individual beetles and beetle populations (Bentz et al. 2009, Sambaraju et al. 2012). Severe drought caused by warm regional temperatures creates water stress in trees, which reduces their ability to take in carbon and decreases resources available for growth, tissue repair, and construction of biochemical defense systems. Thus, under prolonged drought conditions, trees are more likely to succumb to beetles and the threshold number of beetles necessary for a successful attack is reduced (Bentz et al. 2009).

Rising temperatures associated with climate change also reduce constraints on growth of beetle populations, further facilitating eruptions. For instance, eggs and larvae of mountain pine beetles are susceptible to cold-induced mortality during fall and spring when their cryogenic defense mechanisms are minimal (Bentz et al. 1991, 2009). A reduction in cold snaps during these periods directly improves survival rate of eggs, larvae, and brood adults, and thus improves recruitment. Likewise, the spruce beetle life cycle includes pre-pupal diapause during which larval development is paused in late summer and resumes again the following summer after temperatures reach a critical threshold (Schebeck et al. 2017). However, warming temperatures permit diapause omission, resulting in completion of the life cycle in a single year, which can quickly lead to exponential population growth (Hansen and Bentz 2003).

Lodgepole pine and spruce-fir forests in western North America provide habitat for a wide array of mammalian wildlife including game species such as elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*), sensitive species such as Canada lynx (*Lynx Canadensis*) and American marten (*Martes americana*), and foundational members of the subalpine community such as red squirrels (*Tamiasciurus hudsonicus*). Despite the varied and high interest in these species, and the massive changes in their habitat across North America, little has been done to examine the consequences of bark beetle outbreaks on these and other members of the mammalian community. Saab et al. (2014) reviewed literature on response of mammalian species to mountain pine beetle outbreaks in lodgepole forests and found only a handful of works, none of which were peer-reviewed. Most existing literature focused on response of red squirrels, which was generally negative (Stone 1995, Drever and Martin 2007, Mosher 2011). Novel results published by Saab et al. (2014) in addition to their review, and later work by Johnson et al. (2015), confirmed this result. Saab et al. (2014) and Stone (1995) found that red-backed vole (*Myodes gapperi*) response is flat or mixed, and tied mostly to accumulation of coarse woody debris. Stone (1995) also suggested that ungulate species responded positively to mountain pine beetle outbreaks in northern Utah, as did golden-mantled ground squirrels (*Callospermophilus lateralis*), but responses of snowshoe hares (*Lepus americanus*), chipmunk (*Neotamias* spp.), and red-backed voles were muted or mixed. Still, a paucity of published information exists regarding mammalian response to bark beetle outbreaks, especially for species other than red squirrels in systems other than lodgepole pine.

Here, we present an occupancy analysis designed to assess mammalian response to mountain pine beetle and spruce beetle outbreaks in lodgepole pine and spruce-fir forests of the southern Rocky Mountains where over 4 million acres have been impacted since 1994 (USFS Rocky Mountain Region 2018). Specifically, we estimate probability of use of these two forest types by various mammalian species and describe changes in this probability as a function of time elapsed since beetle outbreaks and severity of those outbreaks. Habitat use is fundamental to wildlife ecology as it sets the stage for

survival, reproduction, competition, predation, and other axes encompassed in a species' niche (Morrison et al. 1992). Thus, it is an important and logical starting point to examine response to significant environmental changes induced by bark beetles.

Based on previous work and the natural history and ecology of the species sampled, we expected a variety of direct responses to changes in vegetation (Table 1). However, we also anticipated complex, indirect responses that potentially cascade across trophic levels. For example, we might easily predict a decline in red squirrel use of conifer stands after bark beetle outbreaks due to the loss of cone crops resulting from the death of mature trees (Koprowski 2005, Johnson et al. 2015). In contrast, the response by American marten is more difficult to predict. Martens prey on red squirrels and use their middens as resting and denning habitat (Buskirk and Ruggiero 1994). Thus, like red squirrels, we might expect use to decline in post-beetle stands. However, use of such stands by marten might also increase with expected increases in red-back vole populations (Saab et al. 2014) and availability of coarse wood and large snags, which are important components of marten diet and habitat (Buskirk and Ruggiero 1994). Other important habitat components such as snowpack and subnivean spaces could be impacted by loss of canopy cover; all of these changes could unpredictably impact the competitive abilities of martens compared to other carnivores that use these forests. Thus, our current, broadscale effort is limited to descriptions of observed changes in use associated with beetle outbreaks. We offer potential mechanisms for observed changes where possible, but these should largely serve as hypotheses for future research.

METHODS

Study area

The study area included all subalpine forests (lodgepole pine and spruce-fir) in the state of Colorado (Fig. 1). These forests occurred between 2590 and 3660 m elevation (Benedict 2008:497, 538) in steep and varied topography that generated drastic changes in vegetation over short distances depending on slope, aspect, and elevation. Generally, at the lower end of this

Table 1. Summary of data collected (number of photographs), analysis status (whether data were sufficient to complete the three-step analysis), predicted response to bark beetle outbreaks (generally, without differentiating response through time from response to severity), and rationale for predicted response for species detected via camera traps across a gradient of bark beetle-impacted areas in Colorado, USA, summers 2013–2014.

Species	Photographs	Analysis completed	Predicted response	Rationale for predicted response
American marten (<i>Martes americana</i>)	1901	Yes	+	Increasing coarse woody debris favors primary prey (small mammals) and provides marten habitat; understory development favors secondary prey (snowshoe hares)
Black bear (<i>Ursus americanus</i>)	13,124	Yes	+	New understory vegetation and berry crops provide abundant food
Chipmunk (<i>Neotamias</i> spp.)	2284	Yes	+	New vegetation provides abundant food resources
Coyote (<i>Canis latrans</i>)	1869	Yes	None	Plasticity in behavior, diet, and habitat use allows exploitation of variety of conditions
Elk (<i>Cervus canadensis</i>)	132,953	Yes	+	Abundance of grasses, forbs, shrubs, and saplings provides abundant food and cover
Golden-mantled ground squirrel (<i>Callospermophilus lateralis</i>)	1780	Yes	+	New vegetation provides abundant food resources. Open canopy is preferred habitat
Moose (<i>Alces alces</i>)	2652	Yes	+	Abundance of grasses, forbs, shrubs, and saplings provides abundant food and cover
Mule deer (<i>Odocoileus hemionus</i>)	55,220	Yes	+	Abundance of grasses, forbs, shrubs, and saplings provides abundant food and cover
Porcupine (<i>Erethizon dorsatum</i>)	1246	Yes	—	Diminished supply of live bark and foliage for foraging
Red fox (<i>Vulpes vulpes</i>)	2421	Yes	None	Plasticity in behavior, diet, and habitat use allows exploitation of a variety of conditions
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	17,018	Yes	—	Diminished cone crop causes food scarcity. Several previous works found negative response
Snowshoe hare (<i>Lepus americanus</i>)	17,484	Yes	+	Increasing understory density provides abundant food and cover
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	626	Yes	None	Primary habitat is alpine tundra, talus slopes, and rock outcroppings; forest is secondary
Bobcat (<i>Lynx rufus</i>)	243	No	N/A	N/A
Bushy-tailed woodrat (<i>Neotoma cinerea</i>)	479	No	N/A	N/A
Canada lynx (<i>Lynx canadensis</i>)	26	No	N/A	N/A
Mountain cottontail (<i>Sylvilagus nuttallii</i>)	301	No	N/A	N/A
Mountain lion (<i>Puma concolor</i>)	48	No	N/A	N/A
Mouse (<i>Peromyscus</i> spp.)	336	No	N/A	N/A
Pika (<i>Ochotona princeps</i>)	446	No	N/A	N/A
Raccoon (<i>Procyon lotor</i>)	20	No	N/A	N/A
Striped skunk (<i>Mephitis mephitis</i>)	132	No	N/A	N/A
Vole (<i>Myodes</i> , <i>Microtus</i> spp.)	132	No	N/A	N/A
Weasel (<i>Mustela</i> spp.)	27	No	N/A	N/A
Western spotted skunk (<i>Spilogale gracilis</i>)	22	No	N/A	N/A
Wyoming ground squirrel (<i>Urocyon elegans</i>)	8	No	N/A	N/A

elevation band, or at higher elevations that were drier and/or south-facing, lodgepole pine was the dominant forest cover. At the higher end of this elevation band, and at cool, north-facing slopes at lower elevation, forests were generally

dominated by spruce-fir. Note, however, that lodgepole pine does not occur in the southern third of the state (range limit), and thus, spruce-fir forests were dominant at all elevations and aspects in this portion of the study area. Large

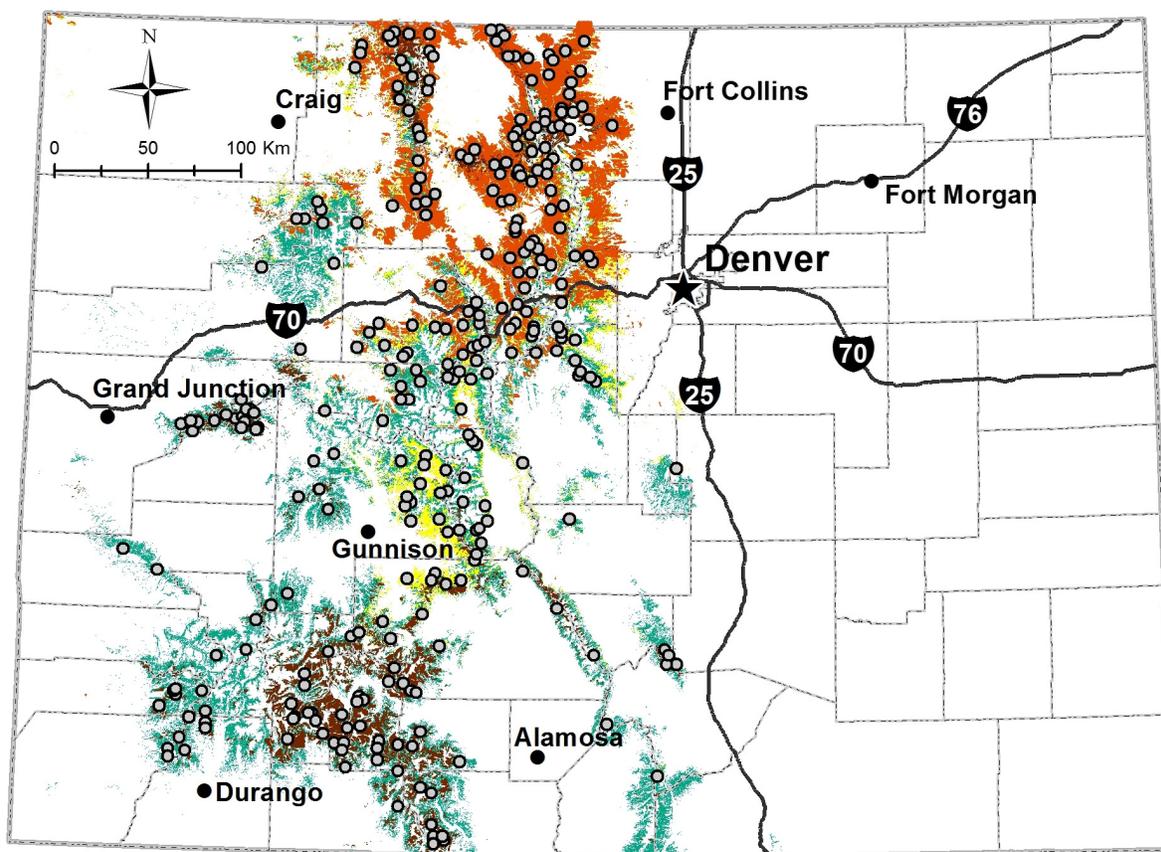


Fig. 1. Randomly selected sampling sites (gray circles) where passive infrared game cameras were deployed in spruce-fir (green) and lodgepole pine (yellow) forests in Colorado, USA, 2013–2014. Brown and orange are the approximate extents of spruce beetle and mountain pine beetle impacts in spruce-fir and lodgepole pine forests, respectively, as of 2014.

aspen (*Populus tremuloides*) stands were interspersed throughout these subalpine forests, depending on disturbance history, soil characteristics, and elevation. Douglas-fir (*Pseudotsuga menziesii*), bristlecone pine (*Pinus aristata*), limber pine (*Pinus flexilis*), and blue spruce (*Picea pungens*) also occurred sporadically where conditions were appropriate. The vegetation band of interest was bordered by alpine tundra above and montane forest consisting largely of Douglas-fir and ponderosa pine (*Pinus ponderosa*) below. Even at these subalpine elevations, forested stands were often dissected by high elevation meadows and open valleys.

We restricted our sampling to public lands managed by the United States Forest Service, National Park Service, Bureau of Land Management, and Colorado State Forest Service. As

such, juxtaposition with human development was minimal outside of scattered seasonal residences, small developments, and occasionally ski runs. However, many subalpine areas were heavily recreated by both motorized and non-motorized users, especially during summer months. Also, many study sites fell within cattle or sheep allotments on public lands.

The climate was typical of continental mid-latitude regions at high elevation (Benedict 2008:149–150). Mean July temperature on the study area was 14.2°C; mean January temperature was –6.1°C. More than half of the annual precipitation (37.7 cm) fell as snow between late October and April, and snow cover often persisted through early June, especially on north-facing slopes. Mean March snow depth across all snonet sites in the study area was 1.3 m. Most of

the annual precipitation that did not fall as snow during winter came as regular afternoon monsoons during mid-late summer (NOAA 2017).

Sampling design

Because this project occurred in tandem with sampling to determine avian response to bark beetle outbreaks, we deployed a 1 km × 1 km grid across the study area to serve as our preliminary sampling frame, as per the Bird Conservancy of the Rockies' protocol for Integrated Monitoring of Bird Conservation Regions (Hanni et al. 2012). We then overlaid a digital elevation model, ownership data, and vegetation data from the Colorado Vegetation Classification Project (CVCP; CPW 2017). From these overlays, we extracted grid cells that occurred on public land, were above 2590 m across ≥75% of the cell, and were comprised of ≥75% spruce-fir or lodgepole pine forest cover. We defined this collection of cells ($n = 15,113$) as subalpine forest in Colorado, and it served as the final sampling frame, or population of cells, to which we sought to make inference (Fig. 1). From this population, we selected a spatially balanced random sample (Stevens and Olsen 2004, Theobald et al. 2007) of $n = 150$ spruce-fir cells and $n = 150$ lodgepole pine cells. Sampling effort was based on a priori power analyses performed on pilot data, which indicated that sampling 125–175 cells would result in an 80% chance of detecting a linear trend in occupancy of 0.03 per year over 15 yr (e.g., if occupancy were to increase steadily from 0.1 to 0.5 or decrease from 0.5 to 0.1).

We constructed histograms of our selection for each stratum, binned by “Years since initial bark beetle outbreak” (YSO), which we estimated from aerial survey data (USFS Rocky Mountain Region 2018). Our initial sample provided a balanced cross section of sites across the YSO gradient for the lodgepole stratum, but overloaded unimpacted sites for the spruce-fir stratum as the spruce beetle epidemic had not yet reached the aerial extent of the mountain pine beetle epidemic. Therefore, to obtain a more balanced representation along the YSO axis, we re-selected grid cells from the spruce-fir stratum as before, but dropped the inclusion probability for unimpacted sites such that the resulting histogram was more evenly distributed along YSO, but still selected randomly and in a spatially balanced

manner. Severity of outbreaks was largely a function of size and species composition such that stands dominated by large lodgepole or large Engelmann spruce trees often experienced high severity when outbreaks occurred, whereas stands with a significant subalpine fir component (or other species) experienced lower severity. We had no way of assessing severity a priori. Our sample ultimately spanned the entire gradient of severity (0–99% of overstory trees impacted) but was skewed toward the lower end of this gradient (mean overstory mortality = 20%).

To assess occupancy of the mammalian community, we deployed a passive infrared camera trap (Reconyx PC800, Holmen, Wisconsin, USA) near the center of each selected 1 km × 1 km cell. Cameras were strapped to a large tree approximately 0.5 m above the ground and pointed toward a lure tree 4–5 m away. We soaked one 1-inch² piece of wool in 15 mL of peanut butter and another in 1 mL of rabbit lure (Pro-Pest Professional Lures, Yazoo City, Missouri, USA), then affixed each to the lure tree with natural twine at 0.5 and 0.25 m above ground, respectively. These small amounts of lure were used to enhance our probability of detecting individuals living locally while minimizing the probability of attracting individuals residing far away. We based the camera configuration and lure selection on pilot work and that of Blecha (2015). Our aim was to maximize our ability to photograph a diversity of species ranging from small-bodied rodents to large-bodied ungulates. We recorded camera trap details as suggested by Meek et al. (2014; Appendix S1: Table S1).

Cameras were deployed in half of the cells in each stratum between 28 May and 24 July 2013 and in the other half of cells in each stratum between 30 May and 21 July 2014. Cameras remained deployed for >4 weeks and were not re-visited until they were retrieved. All photographs were examined by at least two observers (a third observer served as a referee in cases where the first two observers disagreed) using the CPW Photo Warehouse software (CPW; Ivan and Newkirk 2016). After assigning a species to each photograph, we used the software to create encounter histories by binning photographs into discrete occasions beginning the day after the camera was deployed at either noon (nocturnal species) or midnight (diurnal species). We

assigned a “1” to the encounter history string if the species of interest was detected during an occasion or “0” if it was not detected.

There are numerous options for binning continuous data into discrete occasions. Generally, if occasions are too short, estimates of detection probability approach zero, which creates estimation issues, especially for uncommon species. If the overall length of a survey is too long, occupancy estimates approach 1.0, especially for common species, which is an unhelpful outcome when the inferential goal is to parse differential responses of several species to a perturbation. We conducted preliminary analyses to test several binning strategies on both rare and common species in our data set. We settled on seven 4-d occasions as this configuration optimally maintained mean occupancy estimates (i.e., intercept only models) away from boundaries for most species, thus preserving the opportunity to observe changes in both directions (negative or positive) along the YSO or severity axes. This configuration simultaneously maintained estimates of detection probability away from boundaries as well (Appendix S1: Table S2), even for uncommon species. It also aligns with recommendations of (Hamel et al. 2013) who suggested 20–30 problem-free days of camera operation to produce stable and precise estimates of occupancy and detection.

Covariates

In addition to deployment of cameras to detect mammals, avian point counts were conducted at 16 equally spaced (250 m) point locations within each 1 km × 1 km cell. Prior to conducting point counts, observers visually estimated canopy cover by species within 50 m of each point. These field data allowed us to groundtruth strata membership of each cell (i.e., post-stratification), resulting in a spruce-fir:lodgepole pine ratio of 186:114 rather than the 150:150 originally selected based on CVCP data. In addition to obtaining (1) updated stratum data, crews also visually estimated within 50 m of each point: (2) percent of canopy trees that were dead (i.e., severity of outbreak), (3) percent canopy cover of aspen, (4) mean shrub (woody species 0.25–3 m tall, including saplings) height, (5) percent shrub cover by deciduous species, (6) percent shrub cover by coniferous species, (7) percent ground

cover (all material <0.25 m tall) by deadwood >15 cm in diameter, and (8) percent bare ground of all material <0.25 m in height.

Using GIS, we extracted raster (30 m resolution) or polygon data at each of the 16 points in a cell to quantify (1) YSO, based on data collected from United States Forest Service Forest Aerial Detection Surveys (USFS Rocky Mountain Region 2018), (2) topographic wetness index plus (an index of soil moisture based on slope, basin characteristics, and solar radiation; Theobald 2007), (3) topographic position index (an index of concavity or convexity to indicate position along a slope from valley to ridge top; Weiss 2001), (4) heat loading (a measure of the total lumens accumulated at a given pixel over a year, taking into account slope, aspect, and shadows from adjacent landforms; Theobald et al. 2015), (5) elevation, and (6) a binary indicator of whether the cell was in federally designated wilderness or not. For both groups of variables, those collected in the field and those extracted via GIS, we computed the mean across all 16 sample points and assumed this mean adequately represented average forest conditions within the 1-km² cell. We used these means as covariates in an occupancy analysis to determine whether any were related to use of the portion of the forest sampled by the camera trap. Note that home range size matched or exceeded the 1-km² cell size for ungulate and carnivore species in our data set (Armstrong et al. 2011). Thus, use of the area in which the camera was placed might be expected to be influenced by forest conditions at the 1-km² (16-pt) scale. However, rodents and lagomorphs had home ranges <0.2 km² (Armstrong et al. 2011), meaning that many of the 16 points would be outside of the home range of individuals captured by the camera trap. To better scale covariates to space use of these smaller-bodied species, we computed means across the all points within 300 m (generally the 4–5 closest points) of the camera location. Such a radius would conservatively capture a 0.2 km² circle centered on the camera.

Analysis

We fit single-season occupancy models to the encounter data to determine how mammalian species altered their use of subalpine forest stands relative to vegetation changes stemming from bark

beetle activity. As such, the two parameters that required estimation were Ψ , the probability that a sample unit was occupied, and p , the probability that a species was detected in a unit, given that the unit was occupied. In our case, the units were technically the detection zones of each camera (thus we know each cell containing a camera with a detection was “used” to some degree, but we make no assertion that our camera sampled the entire 1-km² cell for each species), and because animals were able to cross into and out of the detection zone of cameras between occasions, our sampling scheme violated the closure assumption of this class of models. Therefore, we interpreted Ψ as the probability that the detection zone of the camera trap was *used* by the species of interest during the course of the survey period (~1 month during summer), as per MacKenzie et al. (2006: page 105). We treated YSO as a group variable, and thus binned encounter data into 12 groups; stands that were still green when sampling occurred were considered “0 YSO,” those impacted by beetles the year prior to our sampling were binned as “1 YSO,” etc.

To efficiently identify the structures and covariate combinations that produced the best fit for each species, we employed a sequential process in the vein of Lebreton et al. (1992). First, we held the Ψ parameter constant at a general structure (i.e., additive model including all covariates) and fit three structures for the detection parameter (p): (1) detection constant across occasions, (2) detection as a linear trend across occasions, and (3) detection as a quadratic trend. The latter models allowed detection probability to decline as lure was washed away by weather or was removed by animals through time. We selected the best-fitting structure for detection using Akaike’s Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002).

Second, after selecting the best-fitting model for p , we then fixed that structure and modeled Ψ by fitting all combinations of four variables from among the 14 listed above (omitting YSO and mortality of canopy trees; see below). This step served to identify a relatively simple model to account for background variability in how species organize themselves across the landscape based on vegetation and topographic variables.

Finally, we fit models to assess our true question of interest: whether covariates related to the

bark beetle epidemic could explain further variation in Ψ over basic models representing Ψ as a function of topographic and vegetation variables. We fixed the best-fitting structures for p and Ψ from steps 1–2, and then added additional structure to Ψ reflecting potential responses to beetle-induced changes in vegetation. Specifically, we hypothesized that species may respond to beetle outbreaks through time (i.e., YSO) by exhibiting (1) no change in their use of forest stands after impact by beetles, (2) a linear increase or decrease in use of stands in the years following impact by beetles, (3) a quadratic increase or decrease in use of stands after impact by beetles, or (4) a response that followed a third-order polynomial form (Fig. 2). We also hypothesized that some species would not begin responding until overstory needles dropped and understory vegetation was released. Therefore, we fit models representing the same general shape as 2–4, but with a delay in the onset of the response until

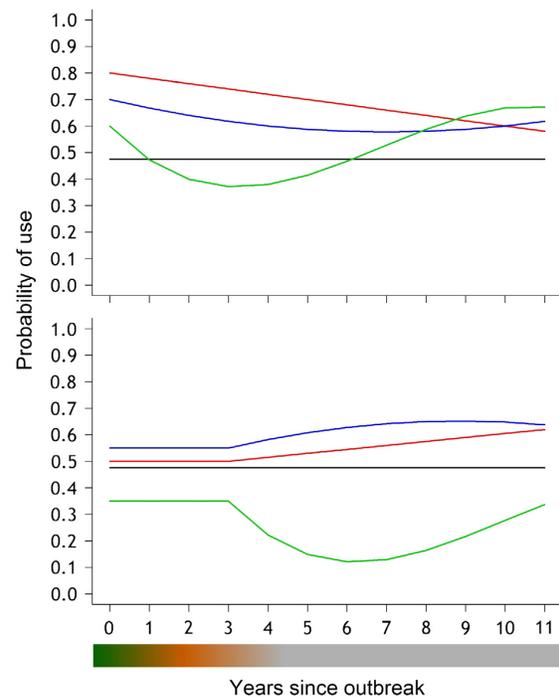


Fig. 2. Example curves fit to occupancy data depicting immediate (upper panel) and delayed (lower panel) response of mammals to bark beetle outbreaks. Actual slopes and inflections were dictated by the specific data for a given species.

3 yr post-beetle impact, which in both forest types was approximately when needles began to drop, canopies opened, and understory changes began (Fig. 2). We assumed that delays in species responses that started >3 YSO would be adequately captured by either quadratic or polynomial models. Additionally, we considered severity of the outbreak as an additive effect that could shift any response up or down, or as an interaction such that the shape of the response itself could change at varying severities. Step 3 of our modeling procedure resulted in 19 models (six plausible response curves, additive or interactive severity combined with each, plus an intercept only model).

We report coefficient estimates for YSO and severity when these occurred as additive effects in best-fitting linear or quadratic models from step 3 (we did not attempt to interpret coefficient estimates from cubic polynomials). However, in the figures we show predicted responses for low (10% tree mortality), medium (50% tree mortality), and high (90% tree mortality) severity averaged across *all* models in the set to fully capture both uncertainty within modeled predictions and that arising from the model-selection process. Our choice of levels for predictions was arbitrary, but covers the full range of severity we observed in the field. We depicted estimates separately for spruce-fir and lodgepole pine stands if the top model from step 2 included a strata effect; otherwise, results were pooled across forest types.

RESULTS

Crews successfully deployed cameras at 273 of the 300 cells originally selected for sampling. Of the 27 cells that were not sampled, 15 occurred in recently burned areas, nine were located predominantly on private inholdings, and three were located on sites that were too dangerous to survey (e.g., too steep, cliff bands). In all cases, replacement cells from the spatially balanced list were substituted for those omitted in order to maintain a sample of 300, which is a strength of the spatially balanced approach, provided that substitution does not happen so often as to impact representativeness of the sample (Stevens and Olsen 2004). Given that we did not intend to make inference to burned areas or private lands,

passing over those units should not have impacted sample integrity. Thus, we feel that the realized sample represented the population of interest as only 1% of the initial selection was omitted due to logistical concerns.

We collected 336,665 photographs of 26 terrestrial mammal species from our sampling effort (Appendix S1: Table S1, Table 1). Of these 26 species, we obtained sufficient data on 13 to complete the analysis specified above (Table 1). Note that for mule deer, coyote (*Canis latrans*), and golden-mantled ground squirrel (*Callospermophilus lateralis*), 1–4 models of the 19 we fit included an interaction between YSO and severity that was not well estimated (i.e., point estimates were unreasonable and/or SEs were several orders of magnitude larger than all other SEs). In each case, we removed these models from the set and made inference from the remaining models.

As per our predictions, elk, mule deer, and moose (*Alces alces*) exhibited a positive association with bark beetle activity, although the nature of these associations varied by species (Fig. 3). Elk use was positively associated with the severity of the outbreak in a given location ($\beta_{\text{Severity}} = 3.37$, 95% CI = [1.38, 5.35]), but there was relatively little association with YSO ($\beta_{\text{YSO}} = -0.05$, 95% CI = [-0.15, 0.05]). Conversely, mule deer were more strongly associated with YSO (use followed a cubic trend that began increasing at about 7 YSO), but this relationship did not change appreciably with increasing severity (Fig. 3). Use of subalpine forests by moose was best modeled by an interaction between YSO and severity. At low severity, mean use was low and nearly flat across the range of YSO (Fig. 3). However, as severity increased, mean use increased in a quadratic fashion and peaked 3–7 YSO ($\beta_{\text{Severity}} = 5.29$, 95% CI = [1.34, 9.34]; $\beta_{\text{YSO}} = 0.66$, 95% CI = [-0.10, 1.42]), though there was considerable uncertainty around this relationship, the majority of which was model-selection uncertainty.

Red squirrel, golden-mantled ground squirrel, chipmunk, and coyote were among the species that exhibited a negative association with beetle activity, but again, responses varied (Fig. 4). The top model for red squirrels was invariant across YSO at low severity, but as severity increased, use declined sharply after 3 YSO ($\beta_{\text{Severity}} = -1.69$, 95% CI = [-3.17, -0.23]), approximately when trees no longer had foliage and cone crops

presumably declined. Red squirrel use was estimated to be about 0.1 (~15%) higher in spruce-fir stands compared to lodgepole stands. As with moose, much of the uncertainty was model-selection uncertainty. Similarly, the top model for golden-mantled ground squirrels included a cubic relationship with YSO and additive impacts of severity ($\beta_{\text{Severity}} = -2.64$, 95% CI = $[-5.89, 0.60]$), although neither effect was particularly evident in the model-averaged output (Fig. 4). Conversely, the top models and model-averaged output for both chipmunk ($\beta_{\text{YSO}} = -0.08$, 95% CI = $[-0.16, -0.00]$) and coyote ($\beta_{\text{YSO}} = -0.14$, 95% CI = $[-0.29, -0.01]$) indicated that use was

negatively associated with YSO, but severity had little impact on occupancy.

Use of subalpine forests by American marten, black bears (*Ursus americanus*), snowshoe hares, and porcupines (*Erethizon dorsatum*) was not substantially influenced by beetle activity (Fig. 5). The top model for each species did not include effects of either YSO or severity. They only included the habitat covariates from the previous modeling step, which resulted in largely “flat” mean responses. However, for snowshoe hares, the second best model had a nearly identical AIC_c score to the top model and included a quadratic relationship with YSO ($\beta_{\text{YSO}} = 0.29$, 95% CI = $[0.00, 0.58]$) such

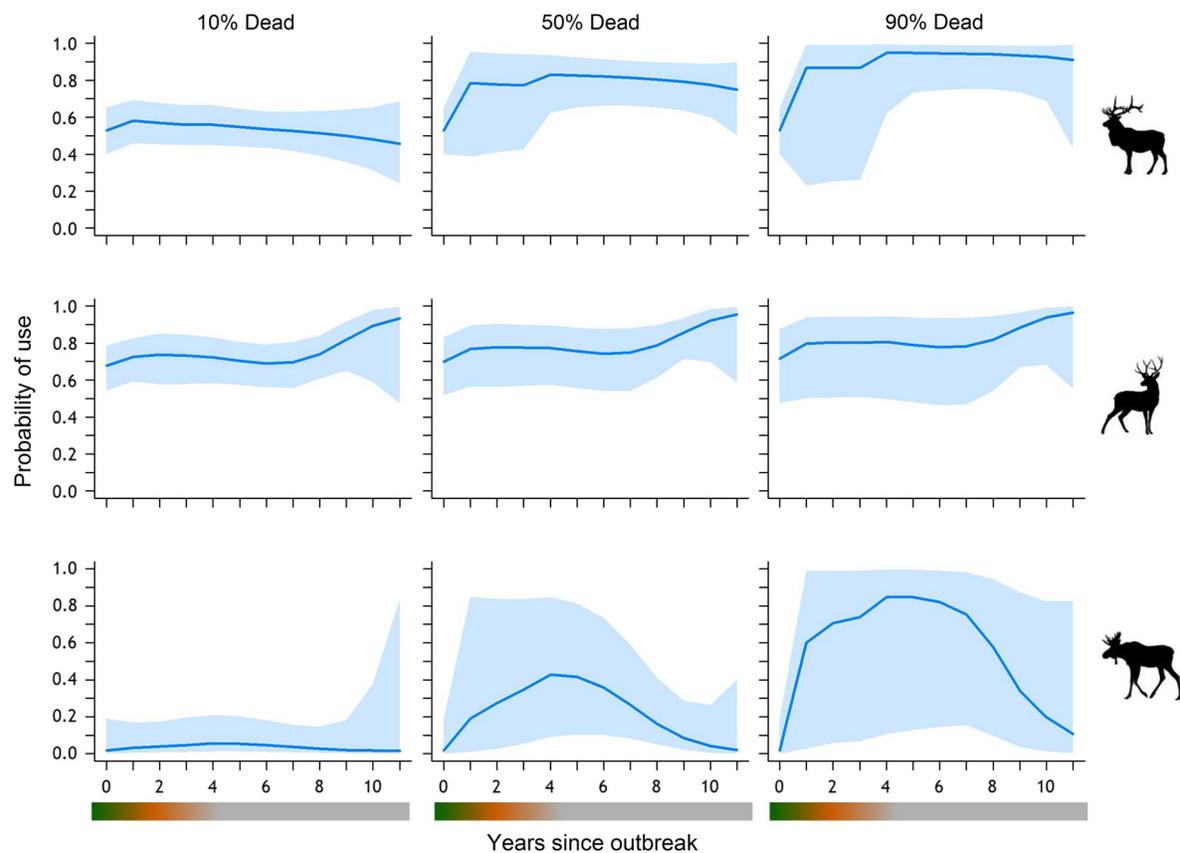


Fig. 3. Mammalian species that exhibited a positive association between use of forested stands and beetle activity (either years since the outbreak occurred, severity, or both). Curves and 95% confidence intervals represent model-averaged responses across all fitted curves described in Fig. 2. From left to right, panels indicate predicted model-averaged responses for cases where 10%, 50%, and 90% of the overstory in a stand is killed by beetle activity. From top to bottom, panels show predicted responses for elk, mule deer, and moose. Probability of use was estimated to vary little between the spruce-fir and lodgepole pine stands, so responses were pooled across habitat types.

that hare use reached a shallow peak approximately 5 yr after beetles first impacted the stand. Some snowshoe hare models that included an interaction with severity also held weight and indicated a weak positive relationship ($\beta_{\text{Severity}} = 4.13$,

95% CI = $[-2.02, 10.28]$), which is why mean snowshoe hare association with YSO was predicted to flatten out at high severity. Snowshoe hare use was estimated to be 0.3 (110%) higher in spruce-fir stands than in lodgepole pine stands.

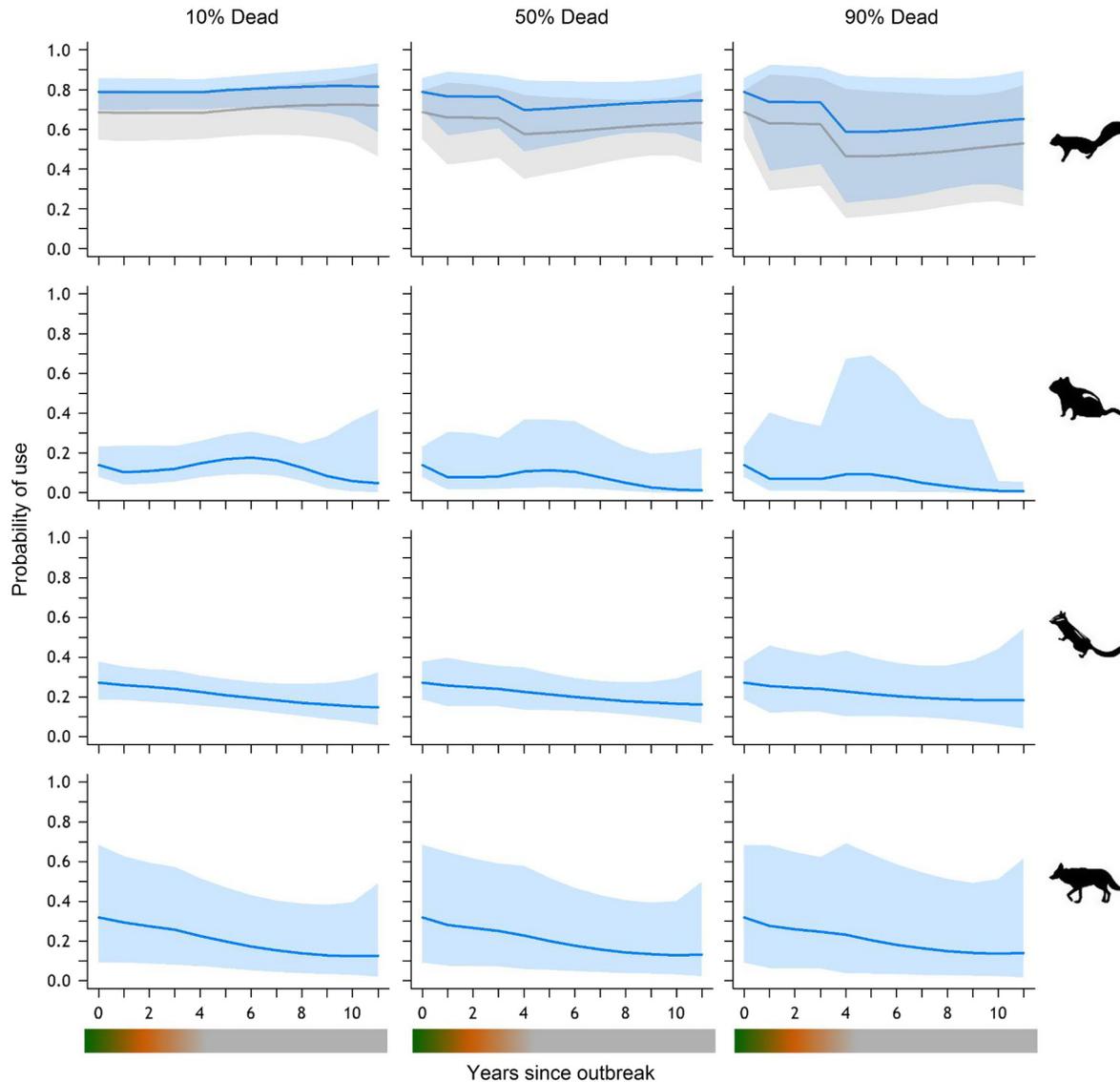


Fig. 4. Mammalian species that exhibited a negative association between use of forested stands and beetle activity (either years since the outbreak occurred, severity, or both). Curves and 95% confidence intervals represent model-averaged responses across all fitted curves described in Fig. 2. From left to right, panels indicate predicted responses for cases where 10%, 50%, and 90% of the overstory in a stand is killed by beetle activity. From top to bottom, panels show predicted responses for red squirrel, golden-mantled ground squirrel, chipmunk spp., and coyote. Red squirrel use was estimated to vary between the spruce-fir (blue) and lodgepole pine (gray) stands. For other species, habitat stratum was less important and responses were pooled across habitat types.

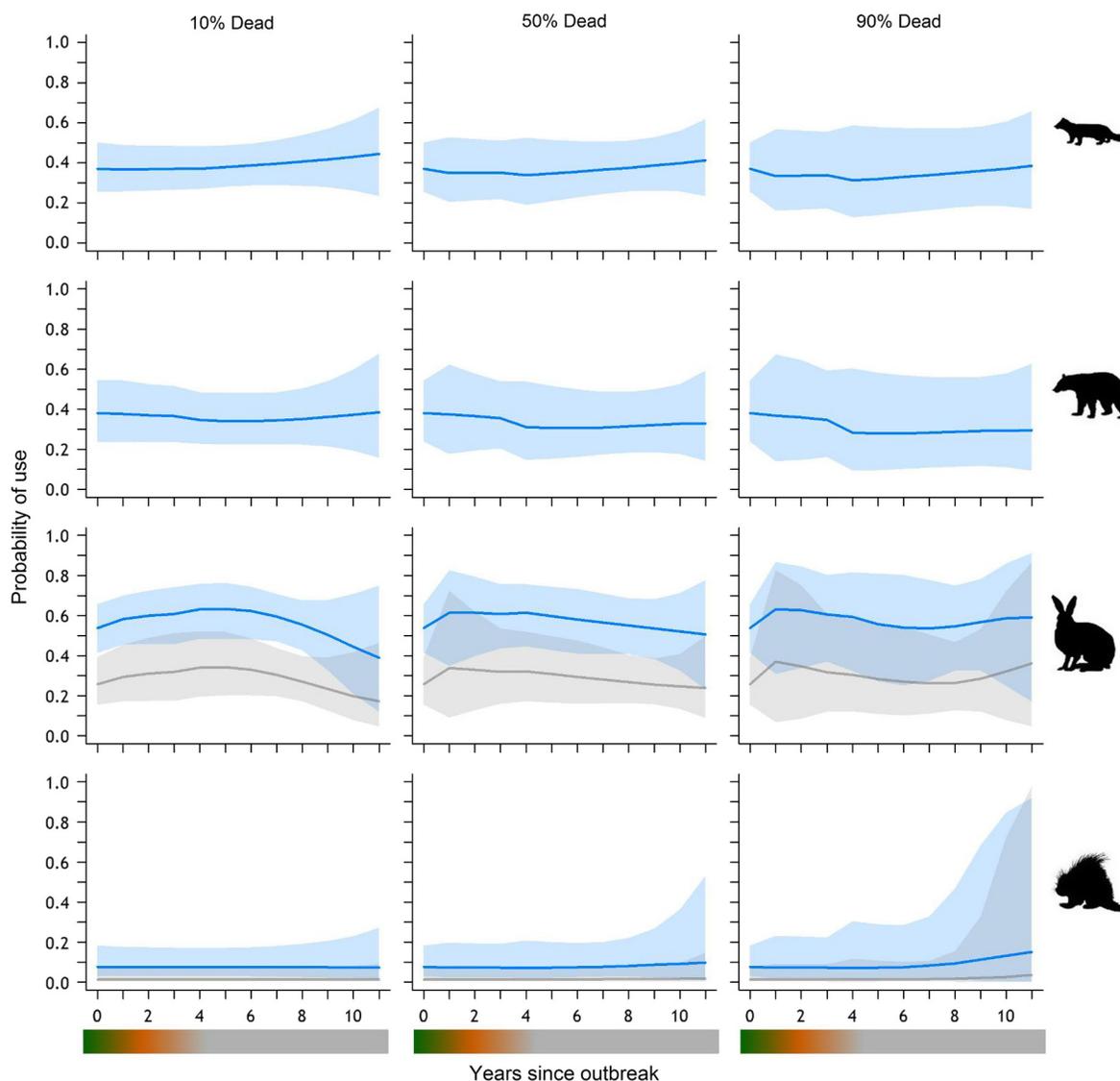


Fig. 5. Mammalian species that exhibited little association between use of forested stands and beetle activity (either years since the outbreak occurred, severity, or both). Curves and 95% confidence intervals represent model-averaged responses across all fitted curves described in Fig. 2. From left to right, panels indicate predicted responses for cases where 10%, 50%, and 90% of the overstory in a stand is killed by beetle activity. From top to bottom, panels show predicted responses for American marten, black bear, snowshoe hare, and porcupine. For snowshoe hares and porcupine, use was estimated to vary between the spruce-fir (blue) and lodgepole pine (gray) stands. For other species, habitat stratum was less important and responses were pooled across habitat types.

Overall porcupine use of subalpine stands in Colorado was the lowest of any species analyzed and was 0.06 (4.5%) higher in spruce-fir than in lodgepole pine stands.

Only two species showed a mixed response to bark beetles along the YSO and severity gradients

(Fig. 6). Red fox (*Vulpes vulpes*) use was positively associated with YSO ($\beta_{\text{YSO}} = 0.08$, 95% CI = $[-0.05, 0.21]$) but negatively associated with severity ($\beta_{\text{Severity}} = -6.24$, 95% CI = $[-12.7, 0.23]$). In contrast, yellow-bellied marmots (*Marmota flaviventris*) were negatively associated with YSO

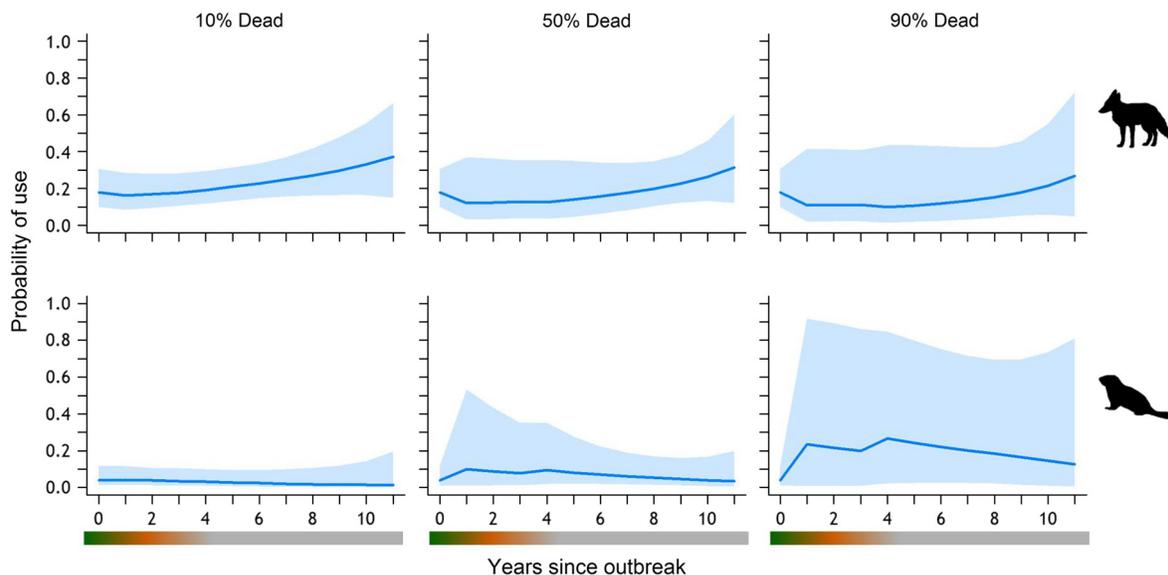


Fig. 6. Mammalian species that exhibited mixed associations between use of forested stands and beetle activity (either positive association with years since the outbreak but negative association with severity, or vice versa). Curves and 95% confidence intervals represent model-averaged responses across all fitted curves described in Fig. 2. From left to right, panels indicate predicted responses for cases where 10%, 50%, and 90% of the overstory in a stand is killed by beetle activity. From top to bottom, panels show predicted responses for red fox and yellow-bellied marmot. Use was estimated to vary little between the spruce-fir and lodgepole pine stands, so responses were pooled across habitat types for these species.

($\beta_{\text{YSO}} = -0.18$, 95% CI = $[-0.43, 0.07]$) but positively associated with severity ($\beta_{\text{Severity}} = 3.65$, 95% CI = $[0.52, 6.77]$). In both cases, however, small changes in mean response were swamped by considerable uncertainty across models.

DISCUSSION

Our sampling entailed the deployment of point-based detectors (cameras sample a relatively small area) in a landscape of continuous space use by the species of interest. That is, our design violated the assumption of closure during the survey period because individuals likely moved into and out of the area sampled by cameras, and therefore sample units toggled between “occupied” and “unoccupied” during each 28-d survey period. This reality necessitated an altered interpretation of the estimates of Ψ as described earlier. Efford and Dawson (2012) noted that under these sampling conditions, Ψ reflects the product of home range area and density, or the “combined ‘footprint’ of the population formed from the union of the home ranges”

overlapping the cameras. Thus, it is impossible to determine whether changes in use presented here reflected changes in density, home range size, habitat use, movements, or some combination thereof.

Despite this, we suggest that our coarse approach is a valuable and informative initial assessment of mammalian response to this large-scale perturbation. Indeed, quantifying intensity of use has long been a staple of ecological investigation (e.g., Manly et al. 2002). Furthermore, sampling at a large scale across a broad array of wide-ranging species leaves one with few choices other than to engage a coarse metric such as “use.” Also, in many cases coarse inference can be honed by invoking species’ ecology. For instance, apparent declines in red squirrel use following a bark beetle outbreak could be due to a reduction in home range size, movement out of impacted stands to unimpacted stands, or reductions in density. However, because this species tends to rely heavily on cone crops as a dietary staple (Armstrong et al. 2011), loss of this food source is unlikely

to lead to a reduction in home range size (if anything, the opposite would occur so that the species could find adequate food resources). Furthermore, the statewide scale of the current outbreaks leaves few opportunities for red squirrels to escape to un-impacted stands. Thus, the most likely explanation is that lower use reflects a reduction in density. Similar understandings of species biology could be used to augment occupancy results, or at least to posit mechanisms for future research. We note that the estimates presented here pertain only to use of these forested areas over a 28-d period during summer. Patterns of use may have differed during other seasons.

Generally, ungulate species exhibited a positive association with bark beetle outbreaks, as we hypothesized, although the shape and nature of their responses were variable. The positive association is likely due to the growth of a diverse and abundant assemblage of grasses, forbs, shrubs, and tree saplings that follows the beetle-induced removal of overstory canopy. Such conditions should be a dietary boon to ungulate species (Wallmo 1981, Toweill et al. 2002, Franzmann and Schwartz 2007). In addition to ample forage, all three species rely on well-distributed cover for escape and loafing behavior during midday. The thick understory regeneration present in the most severely impacted forests could provide this needed cover near an abundant food source, increasing use of these stands (Wallmo 1981, Toweill et al. 2002, Franzmann and Schwartz 2007). These results are consistent with Stone (1995) who noted a positive linear relationship between fecal pellet groups of ungulates and outbreak severity following a mountain pine beetle epidemic in Utah. Notably, we found that mule deer responded to YSO, but not severity, which was a strong, positive predictor of elk and moose responses. Severity was included in each of the four models that were discarded from the mule deer analysis because parameters were not well estimated. In each model, evidence suggested that the direction of the severity effect was positive, same as for elk and moose. Thus, it is likely that mule deer use of beetle-impacted stands was positively associated with severity, but our particular data set prevented this association from surfacing in a well-estimated manner.

Use of beetle-impacted subalpine stands by moose was negligible in low-severity conditions, but in mid- to high-severity conditions, mean use increased after a bark beetle outbreak, followed by a sharp decline 7–8 yr later. We observed significant variation about this mean response, which was due mostly to model-selection uncertainty (i.e., the top models included a quadratic effect that was significantly different from zero, but competing models without this effect also had weight). In Colorado, subalpine forest stands provide secondary habitat for moose, with primary habitat being forest edge and adjacent wet meadows and willow (*Salix* spp.) carrs (Armstrong et al. 2011). Thus, the observed pattern could reflect moose taking advantage of the adjacent flush of new growth when convenient, but electing their preferred habitat once navigation in forest habitats becomes difficult due to dense vegetation and/or down wood, or to decline in nutritional value of regenerating understory. Use of subalpine stands was negatively associated with shrub height based on the top model from step 2 (Appendix S1: Table S3), possibly lending some support to either mechanism. Regardless of mechanisms driving ungulate responses, it appears that ecologists and managers can expect an increase in ungulate use of beetle-killed stands, especially those that were severely impacted. Such changes, whether due to an increase in abundance and/or changes in habitat use, could influence a variety of processes such as regeneration rates of forests and understory, species composition of regenerating forests and understory, space use and density of predators, and dispersion of the hunting public on the landscape during early seasons (e.g., August, early September).

As noted earlier, red squirrels exhibited the strongest negative response to bark beetle outbreaks of any of the species sampled, especially in high-severity locations. We suggest the observed decline in use in highly impacted areas reflects a decline in squirrel density related to diminished cone crops, which are a staple in the red squirrel diet (Armstrong et al. 2011). Golden-mantled ground squirrels and chipmunk spp. were also negatively impacted, but not to the same degree. Like red squirrels, their diets include seeds, but also a variety of other items including forbs, buds, and insects (Armstrong

et al. 2011) which may buffer their response compared to red squirrels. Also, top models for both golden-mantled ground squirrels and red squirrels included a positive relationship with bare ground, suggesting that part of the negative response to beetle impacts may simply be related to an aversion to dense vegetation at ground level. Johnson et al. (2015) summarized the foundational roles that red squirrels fulfill in the subalpine forest community including impacts to small mammal and carnivore communities via their midden-building activities (Ruggiero et al. 1998, Pearson and Ruggiero 2001), avian communities via nest predation (Siepielski 2006), the vegetation community via their influence on cone serotiny (Benkman and Siepielski 2004), and predator communities via their role as prey for several species including northern goshawks (*Accipiter gentilis*), American marten, and others (Buskirk and MacDonald 1984, Squires 2000). Thus, declining red squirrel use of beetle-impacted subalpine forests could result in cascading changes throughout the system, at least until cone crops recover.

Observed responses of several other species did not track our predictions. We expected black bears to respond positively to the flush of new grasses, forbs, shrubs, and berries available in beetle-impacted forests, but their response did not vary with YSO or severity. Perhaps their high mobility and propensity to exploit a variety of habitats precluded a strong response to changes in subalpine forest. We also expected snowshoe hares to respond strongly to understory release, but their response was muted. Yeager and Roridan (1953) and Stone (1995) likewise predicted a positive response for snowshoe hares, yet observed an equivocal one. We note that nearly all of the top models from step 2 of our analysis of snowshoe hares included a positive effect of "bare ground." Perhaps increasing foraging opportunities for hares associated with increased density of conifer saplings in beetle-impacted stands were offset by a lack of bare ground in these stands, which may have impeded locomotion. Alternatively, positive responses to increased conifer density in some stands could have been offset by negative response to tall, dense grass and forb regeneration in others (understory regeneration can be highly variable from site to site depending on conditions). We expected

martens to be positively associated with beetle-impacted stands based on expected increases in small mammal prey (i.e., red-backed voles; Stone 1995, Saab et al. 2014) and coarse woody debris (Armstrong et al. 2011), but did not observe this. Perhaps mixed (snowshoe hare) to negative responses (red squirrels) of other prey items mitigated use of impacted stands or more complex relationships with competitors or altered habitat features muted their response. We expected a negative response from porcupines, but instead observed a flat response, and maybe more importantly, almost no porcupine observations in the study area despite a relatively high probability of detection (Appendix S1: Table S2). The small number of detections in subalpine forests in Colorado matches recent observations in Montana (Mally 2008), Arizona (Brown and Babb 2009), and potentially California (Allen and Casady 2012, Appel et al. 2017).

Given the plasticity in behavior, diet, and habitat exploitation displayed by coyotes and red foxes (Armstrong et al. 2011), we expected no response to bark beetle outbreaks. We also did not expect to detect yellow-bellied marmots at our camera stations, let alone observe a response to beetles, given that they typically reside in tundra and talus habitats (Armstrong et al. 2011). However, coyotes and red foxes did show at least some association with either YSO, severity, or both. Coyotes were negatively associated with shrub height (Appendix S1: Table S3), so perhaps changes in vegetative structure drove their declining use of beetle-impacted forests. We cannot posit a mechanism for the mixed response exhibited by red fox. We do, however, suggest that the peaked use of severely impacted forest stands by marmots may reflect foraging forays from preferred talus slopes and rock outcroppings into adjacent forest to exploit new vegetative growth, similar to the pattern and mechanism we suggested for moose.

Our work is among the first to quantify the response of a suite of mammalian species to the extensive bark beetle outbreaks that have impacted much of western North America. We demonstrated that the magnitude and direction of responses, as well as the role of outbreak severity and elapsed time since inception of the outbreak, vary widely among species. This result was expected given the diversity of taxa examined,

although many of our species-specific findings did not track our a priori predictions. We discussed possible mechanisms for these observed responses, further evaluation of these hypotheses is required. Our inferences were based on a relatively coarse metric, and we suggest that future work include intensive efforts to determine impacts to density, survival, and recruitment of key species, impacts to species richness and community assemblages, and direct tests of intermediate disturbance hypotheses.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2369/full>