DEMOGRAPHIC RESPONSES OF WOODPECKERS IN RELATION TO A MOUNTAIN PINE BEETLE EPIDEMIC IN THE ELKHORN MOUNTAINS OF MONTANA

by

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ABSTRACT

Mountain pine beetle (*Dendroctonus ponderosae*; MPB) epidemics in coniferous forests of western North America have recently increased in size and severity, which affects wildlife habitat. Development of meaningful habitat-conservation strategies therefore requires information on wildlife population responses to mountain pine beetle. Over nine years (2003-2006, 2009-2013), we monitored 355 nests of 5 woodpecker species: American three-toed woodpecker (*Picoides dorsalis*), hairy woodpecker (*P. villosus*), downy woodpecker (*P. pubescens*), red-shafted northern flicker (*Colaptes auratus cafer*), and red-naped sapsucker (*Sphyrapicus nuchalis*) in the Elkhorn Mountains of Montana. In our study area, a MPB epidemic began in 2006 and peaked in 2008. We investigated the relationships between daily survival rate (DSR) and metrics of epidemic severity and timing (epidemic period, annual and cumulative estimates of tree-mortality, and red squirrel [*Tamiasciurus hudsonicus*] counts) while accounting for other potentially important covariates identified in previous studies (temperature, precipitation, time within the breeding season, nest height, diameter at breast height of the nest tree, and nest-tree species). Additionally, we examined trends in densities of hatched nests concurrent with the epidemic. In general, we found little support for a relationship between DSR and variables that described MPB epidemic timing and severity. Red-naped sapsucker was the only species to show a relationship between DSR and a MPB-related variable (cumulative tree-mortality). In contrast, densities of hatched nests for American three-toed, hairy, and downy woodpeckers increased following the epidemic, whereas, nest densities for red-naped sapsucker did not change. We found stronger support for nest survival relationships with covariates unrelated to the MPB epidemic (temperature, nest height, diameter at breast height of the cavity tree), but even these relationships were only weakly supported. As is commonly the case for cavity-nesting birds, nest survival was relatively high, leaving little room for covariate relationships. Our findings suggest that woodpecker populations tend to relate positively with MPB epidemics, although these relationships may often be the result of numerical increases in nest densities rather than functional increases in nest survival rates.

INTRODUCTION

The conifer-dominated forests of the Intermountain West are valued not only because of recreational opportunities, watershed services, and timber resources that they provide across diverse forests types, but also for the crucial habitat that they furnish to the region's iconic wildlife. Disturbance cycles in western North American forests, often caused by agents such as wildfire, insects, and pathogens, are naturally-occurring processes crucial to forest health that, in recent years, have been altered by climate as well as fire and timber management practices (Attiwill 1994, Parker et al. 2006, Raffa et al. 2008, Bentz et al. 2010). Current and future mountain pine beetle (*Dendroctonus ponderosae*) epidemics will likely impact the region's coniferous forests by modifying fire regimes and timber management practices, as well as affecting nutrient cycling, watershed processes, and wildlife habitat (Safranyik et al. 2006, Kaufmann et al. 2008). To make informed forest management decisions regarding forests affected by large-scale beetle disturbances, a clear understanding is needed of bark beetle effects on populations of wildlife (Saab et al. 2014).

The mountain pine beetle (MPB) is a native bark beetle that is typically present in low (i.e., endemic) numbers in coniferous forests where it colonizes several host tree species (primarily *Pinus* spp.) including lodgepole and ponderosa pine (*Pinus contorta* and *P. ponderosa* respectively; Sartwell and Stevens 1975, Safranyik et al. 2006). At endemic levels, MPB is responsible for the mortality of a small number of susceptible host trees and it is in direct competition for resources with a variety of other insect species (Powell et al. 2012). During epidemic years, however, large numbers of individuals can overcome the defenses of host trees, resulting in large, landscape-scale mortality across thousands of hectares of forest (Sambaraju et al. 2012). Recently, areas of western North America have seen the most severe beetle

epidemics in recorded history (Bentz et al. 2010). In British Columbia, MPB has caused the death of lodgepole pine over more than 18 million ha[1] in the past two decades, including a single epidemic between 1999 and 2005 that affected more than 7 million ha (Aukema et al. 2006). These recent epidemics are due, in part, to large areas of pine forest containing high concentrations of MPB-suitable host trees (esp. lodgepole; Kaufmann et al. 2008). Additionally, recent climate warming trends have resulted in higher average winter temperatures and reduced occurrence of extreme bouts of cold temperatures (i.e., ≤ -35 °C) thereby decreasing the threat of cold-induced mortality for various MPB developmental life-stages (a key MPB population limiting factor; Régnière and Bentz 2007, Bentz et al. 2010, Sambaraju et al. 2012). Furthermore, climate models predicting warmer temperatures this century show that the habitable range of MPB will shift north and to higher elevations, such that MPB will affect areas not previously at risk of MPB disturbance (Williams and Liebhold 2002, Bentz et al. 2010, Sambaraju et al. 2012).

The effects of MPB disturbance on forest vegetation are not only highly visible, but well-studied; however, the impacts that these changes pose to wildlife are not clear, in part, due to a wide range of potential species-specific responses (Saab et al. 2014). For avian cavity-nesting species, such as woodpeckers, beetle epidemics can be beneficial because of pulses in snags that provide increases in nesting substrate and food resources. The benefits received by woodpeckers resulting from MPB disturbance may be important, not only to individuals (i.e., increased adult survival and fecundity), but also to populations (i.e., by creating source populations; Ostfeld and Keesing 2000, Runge et al. 2006). Previous research in British Columbia reported no changes in measures of fecundity (quantified by clutch size and mean

[1] British Columbia Ministry of Forests, Lands and Natural Operations 2012: http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/facts.htm

number of fledglings per nest), but provided evidence that woodpecker abundance and nest densities increased as a result of a MPB epidemic (Edworthy et al. 2011).

Persistent woodpecker populations are important to forest ecosystems (Virkkala 2006). Many cavity-excavating woodpeckers are considered keystone species because they excavate cavities that are subsequently used by a diversity of other wildlife taxa (Martin and Eadie 1999, Martin et al. 2004). As a result, some studies show that woodpeckers can be used as indicators to monitor changes in forest biodiversity (Mikusiński et al. 2001, Virkkala 2006, Drever and Martin 2010). Woodpeckers are considered sensitive species by many state and federal agencies because they are responsive to forest management activities (Saab et al. 2007). Management actions proposed to address MPB disturbance will potentially impact woodpecker populations, and range from thinning forests in an effort to reduce future susceptibility of MPB colonization, to salvage logging in MPB-killed forests (Safranyik et al. 2004, 2006, Lindenmayer and Noss 2006, Lindenmayer et al. 2012). Regardless of the proposed action, managers are often challenged with balancing the goals of harvest, while protecting and maintaining biodiversity (Saab et al. 2014).

In this study, we focused on two demographic measures of woodpecker populations in relation to a MPB epidemic: daily nest survival rates (i.e., the probability that a nest will survive one day; DSR) and nest densities (number of nesting attempts in a given area). We have two questions of interest: 1) Do woodpecker nest survival rates (i.e., DSR) change in relation to a MPB epidemic? 2) How do woodpecker nest densities change as a result of a MPB epidemic?

Species and Predicted Responses

We focused this investigation on 5 nesting woodpecker species: American three-toed, hairy, and downy woodpeckers (*Picoides dorsalis*, ATTW; *P. villosus*, HAWO; and *P. pubescens*, DOWO, respectively); northern flicker (*Colaptes auratus cafer,* NOFL; red-shafted sub-species); and red-naped sapsucker (*Sphyrapicus nuchalis*, RNSA). Based on differences in life history traits regarding food acquisition and nesting preferences, we hypothesized relationships between population parameters (i.e., nest survival and nest density) and variables related to a MPB epidemic for all species.

ATTW is a disturbance specialist, particularly among the three *Picoides* species in this study, typically found in montane and boreal coniferous forests (Leonard 2001). The main food resource for ATTW is adult and larval bark beetles of the genus *Scolytidae* (including MPB). This woodpecker is well adapted to making superficial excavations into trees to access galleries containing adult and larval bark beetles in the cambium layer, although ATTW will feed on adult and larval forms of wood boring beetles as well (e.g., families *Cerambycidae* and *Buprestidae*; Leonard 2001). Anatomical differences in ATTW compared with many other *Picoides* species include an increased musculature associated with hammering force (Leonard 2001). These adaptations are not likely necessary for feeding mechanics, but instead for creating nest cavities in trees and snags with little decay. Consequently, ATTW is characterized as a strong excavating species (Leonard 2001, Martin et al. 2004). For these reasons, ATTW is able to take advantage of pulses of high food availability and will excavate nest cavities in recently killed snags centralized in areas of high insect disturbance.

DOWO is the smallest-sized woodpecker of the three *Picoides* species in our study. Due to a small forceps-like bill, the main foraging techniques of DOWO include gleaning from leaf

and bole surfaces and making small superficial excavations into the bark and cambium of trees in search of shallow sub-surface prey (Jackson and Ouellet 2002). DOWO is known to focus its feeding on bark beetles (especially during epidemics) employing its ability to access galleries just under the surface of the bark (Jackson and Ouellet 2002). DOWO is categorized as a comparatively weak excavating species because of its smaller bill in relation to other *Picoides* species (Martin et al. 2004). Consequently, DOWO is more closely tied to deciduous forest types for nesting substrate (e.g., quaking aspen, *Populus tremuloides*; hereafter, aspen), where it favors decayed trees and snags (Martin et al. 2004).

HAWO is a widely-distributed woodpecker that exhibits the most generalized feeding and nesting habits of the *Picoides* species studied (Jackson et al. 2002). Foraging styles include gleaning from the bark surface; superficial bark scaling; excavation of small to large holes in bark, cambium, and wood of trees; sap, fruit, and seed foraging; and fly-catching on the wing (Jackson et al. 2002). Despite this varied foraging skill set, HAWO is known to focus feeding on eruptive abundances of insects such as bark beetles (e.g., MPB, Jackson et al. 2002). Nesting substrates selected by HAWO are described as opportunistic based on the availability and abundance of preferred tree species with appropriate decay (Jackson et al. 2002). This species also is categorized as a strong excavating species (Martin et al. 2004) enabling it to create nesting cavities substrate with little decay amid areas of high insect disturbance.

We considered demographic responses for these three *Picoides* species (i.e., ATTW, HAWO, and DOWO; hereafter referred to as *Picoides* spp.) to be similar because their main food resource is adult and larval stages of bark and wood-boring beetles obtained by excavating trees and snags (Leonard 2001, Jackson and Ouellet 2002, Jackson et al. 2002). All three *Picoides* woodpeckers are resident species (i.e., year-round occupant), probably due to the year-round

availability of their insect prey. We hypothesized that DSR of *Picoides* spp. would be positively associated with a MPB epidemic because of the resulting pulse in snag resources. Accordingly, we expected nest densities of *Picoides* spp. to be positively associated with a MPB epidemic as well because of immigration from areas with low resource availability and decreased distance of juvenile dispersal within the area affected by MPB disturbance.

NOFL is considered a ground-foraging woodpecker because it feeds primarily on ground-dwelling arthropods (mainly adult and larval ants; family *Formicidae*), but is also known to consume adult and larval beetles, as well as a variety of fruits and seeds (Wiebe and Moore 2008). We expected the primary foraging substrates (i.e., downed logs) and associated prey items (ants) of NOFL to be positively affected by the MPB epidemic (cf. Bull et al. 2007). NOFL is considered a migratory species (possibly as a consequence of the seasonal availability of its food resources); however, some individuals might exhibit short, local movements to lower elevations in search of food (Wiebe and Moore 2008). NOFL has comparatively weak excavator morphology and consequently, relatively soft wood appears to be a major determinant of its nest site characteristics. In western North America, NOFL tends to favor nesting in decay-prone *Populus* spp. woodlands (especially in aspen groves), but will nest in *Pinus* spp. of suitable decay (Wiebe 2001, Aitken et al. 2002, Martin et al. 2004, Wiebe and Moore 2008). We hypothesized that DSR and nest densities for NOFL would be positively associated with MPB disturbance because snags created by a MPB epidemic would provide increased foraging and nesting substrate.

During the breeding season, RNSA obtains the majority of its energetics by consuming sap and cambium of coniferous and deciduous trees. This species also opportunistically feeds on insects that are trapped in sap (especially ants and small flying insects) and performs short

fly-catching forays to capture winged arthropods (Walters et al. 2002). Feeding requirements of RNSA place them in close association with live trees (often in aspen woodlands) as compared with *Picoides* spp. and NOFL. Probably as a consequence of their seasonally available food, RNSA is the only strict migrant of the five woodpeckers investigated. In addition to foraging heavily in deciduous woodlands, RNSA predominantly nests in live aspen and is considered a weak cavity excavator compared with *Picoides* spp. (Dobkin et al. 1995, Martin et al. 2004). We hypothesized that DSR and nesting densities of RNSA would remain unaffected by a MPB epidemic because nesting and foraging habitat (i.e., aspen woodlands) are not directly affected by MPB.

Predicted Nest Survival Covariate Relationships

The ecological literature is relatively rich with studies investigating relationships between reproductive success of cavity-nesting birds and abiotic and biotic variables (Li and Martin 1991, Martin and Li 1992, Saab and Vierling 2001, Mahon and Martin 2006, Bonnot et al. 2008, Kozma and Kroll 2010, Edworthy et al. 2011, Newlon and Saab 2011, Saab et al. 2011, Straus et al. 2011). Within this body of knowledge, studies quantifying DSR of nests are common due to the recent advent of useful methodology that produce these estimates (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004, Stephens et al. 2005). Here, we identify variables previously reported to affect DSR of cavity-nesting species, that we considered important in our study, as well as covariates related to a MPB epidemic. We provide hypotheses, including the expected direction of relationships, between covariates of interest and DSR for nests of focal woodpecker species.

We considered three different hypotheses relating DSR and time within the breeding season (hereafter day-of-season) for all species. First, we hypothesized that variation in DSR throughout the season would be best explained as constant because nest survival rates of cavity-nesting birds are high compared to that of other small landbirds (perhaps due to benefits of a fortified nest; Martin and Li 1992). We also considered the hypothesis that DSR varies positively with linear day-of-season due to time constraints within the breeding season resulting in more aggressive parental behavior toward predators later in the season (Biermann and Robertson 1981). Finally, we hypothesized that DSR would be lower during mid-season if predators focused their efforts on the abundance of avian nests available during that time (Dinsmore et al. 2002).

We expected the relationship between DSR and maximum daily temperature to vary by species owing to differences in nest-site preference. Previous studies have shown that cavity microclimate is highly influenced by ambient temperature, and that eggs and nestlings are sensitive to extreme high temperatures (Wiebe 2001, Amat-Valero et al. 2014). *Picoides* spp. were expected to choose nests sites in areas of high snag density (*Pinus* spp.) and accordingly, their nests might be subjected to higher ambient temperatures associated with dead and denuded areas of forest (cf. Saab et al. 2011). Hence, we hypothesized that DSR would decrease with increased maximum daily temperatures for *Picoides* spp. Conversely, nest sites preferred by RNSA and NOFL (i.e., aspen) are placed in relatively cooler, more shaded, aspen woodlands that might provide better protection from extreme heat than nests placed in areas characterized by relatively low forest canopy cover (Walters et al. 2002, Raffa et al. 2008, Newlon and Saab 2011). Because NOFL and RNSA nest sites tend to be in cooler microhabitats, we hypothesized that warmer maximum daily temperatures would increase insect activity and create more

opportunities for insect foraging, thereby increasing DSR of nests for these two species (Honek 1997, Towler et al. 2012).

We expected that higher amounts of precipitation would negatively affect DSR for RNSA. Previous studies have supported the negative effect of increased short-term precipitation on DSR in avian species primarily due to decreased foraging opportunities to feed nestlings (Roberts and Porter 1998, Dinsmore et al. 2002, Moynahan et al. 2007, Newlon and Saab 2011, Saab et al. 2011, Skagen and Adams 2012). We hypothesized that increased amounts of short-term precipitation would decrease flying arthropod activity resulting in fewer feeding opportunities for RNSA (Neal et al. 1993, Saab et al. 2011). Specifically, the effect of lagged precipitation (i.e., previous day's rainfall amount) was predicted to decrease DSR the following day for RNSA in two ways: 1) by increasing the possibility of nestling death from attrition due to parental abandonment (Neal et al. 1993); and 2) by increasing the risk of nest predation resulting from lower vigilance at the nest due to more frequent foraging trips to feed nestlings after rain events (Moynahan et al. 2007).

We did not expect foraging opportunities for *Picoides* spp. to be affected by higher amounts of precipitation because the activity of larval bark beetles (the stage of MPB most commonly consumed) is not be affected by short-term precipitation patterns (B. Bentz pers. comm., 2014). Increased short-term precipitation was not expected to decrease foraging opportunities for NOFL because this would not impair their ability to excavate ant colonies and obtain adult and larval stages (Wiebe and Moore 2008).

We hypothesized that nest tree genus would affect nest survival. More specifically, we predicted DSR for nests of *Picoides* spp. to be lower in aspen than in *Pinus* spp. (ponderosa and lodgepole pine). Nests placed in aspen were expected to be less centrally located within areas

of high food resources (i.e., MPB) compared with nests placed in *Pinus* spp. (Leonard 2001). We expected nest placement amid high resources (i.e., conifer snags) to outweigh the potential consequences of higher temperature and increased predation risk from mammalian predators, specifically American red squirrel (*Tamiasciurus hudsonicus*, RESQ), which are found in greater abundance in coniferous forests (Tewksbury et al. 1998). DSR for nests of NOFL and RNSA, however, was hypothesized to be higher for nests in aspen because of lowered predation risk resulting from high nest densities in aspen woodlands (Li and Martin 1991, Dobkin et al. 1995, Aitken et al. 2002, Aitken and Martin 2004, Martin et al. 2004). One explanation to account for our expectation of lower predation in areas of high nest densities was proposed by Martin (1993) and called the "potential-prey-site hypothesis" and postulated that an increased number of potential nest sites may increase the search time needed for predators to effectively find occupied nests. Additionally, some excavator species (e.g., NOFL and RNSA) aid in this "swamping" effect by excavating several roosting and potential nest cavities annually when preferred nesting substrates are available (Wiebe and Moore 2008). Furthermore, increased vigilance of nearby nesting birds may also decrease predation risk (Brown and Brown 1987, Moynahan et al. 2007), and this is expected to be highest in aspen groves where high concentrations of avian species nests are typically found (Brown and Brown 1987, Moynahan et al. 2007).

Nest height was hypothesized to be positively associated with DSR of nests for all species because higher nests are more difficult to access by ground-based nest predators (Best and Stauffer 1980, Nilsson 1984, Li and Martin 1991, Fisher and Wiebe 2006, Saab et al. 2011). We also expected DSR be positively related with diameter-at-breast height of the nest tree (DBH) because of the buffering capacity against temperature extremes (i.e., better

thermoregulation of nest contents) and better structural protection against predation (i.e., thicker cavity walls; Dobkin et al. 1995, Joy 2000, Wiebe 2001, Amat-Valero et al. 2014).

Previous research regarding population and demographic parameters of woodpeckers (including occupancy, relative densities, nest survival, and fecundity) has suggested that responses to MPB epidemics vary by species (Saab et al. 2014). We hypothesized DSR for nests of *Picoides* spp. and NOFL to be positively associated with MPB epidemic period (i.e., categorically; before or after), whereas DSR for nests of RNSA would remain unaffected. Our expectations regarding the effect of MPB disturbance on DSR follow that *Picoides* spp. and NOFL will directly benefit from increases in food resources and nesting substrates resulting from an epidemic, whereas resources for RNSA would remain constant with respect to MPB disturbance.

Snag densities, both at local- and landscape-scales (i.e., nest and home range, respectively), surrounding nests were expected to be positively associated with DSR for *Picoides* spp. and NOFL because of increased food and nesting resources provided by snags (e.g., conifers killed by MPB; Saab et al. 2007). Additionally, high snag densities surrounding nest sites may allow adults to maximize their vigilance and protect their nests more effectively by spending less time in transit between foraging excursions. We expected no association between DSR of RNSA and snag densities because food and nesting resources for this species would remain largely unaffected by MPB epidemic conditions. Furthermore, we predicted that local-scale snag density estimates should influence DSR more strongly because they represent differences in nest site preference among species better than landscape-scale measurements. As a consequence, we expected RNSA to select nest sites with low local-scale snag density, whereas *Picoides* spp. and NOFL were predicted to select higher snag densities at the local-scale (Hutto 1995, Bonnot et al. 2009, Saab et al. 2009).

RESQ is a diurnal tree squirrel found throughout North America and is associated with coniferous forests in the Western US where it feeds, primarily on seeds from coniferous trees and mycorrhizal fungi (Steele 1998). Although RESQ is primarily granivorous, the species is known to opportunistically depredate nests of cavity-nesting birds to feed upon eggs, nestlings, and in some cases adult birds (Li and Martin 1991, Martin 1993, Steele 1998, Tewksbury et al. 1998, Paclík et al. 2009). We hypothesized that increased RESQ density surrounding a nest site would be negatively associated with DSR for all species. Few studies have investigated population level responses of RESQ to MPB epidemics, but RESQ abundance was reported to be negatively impacted by epidemic conditions (Saab et al. 2014). We also expected estimates of RESQ abundance to decrease in relation to MPB disturbance and, therefore, considered this covariate separately from other MPB related measures. Other predators present on our study units that have been observed or implicated in depredating nests of cavity-nesting birds include American black bear (*Ursus americanus*), northern flying squirrel (*Glaucomys sabrinus*), and yellow-pine chipmunk (*Tamias amoenus*). However, estimating densities of these species was not within the logistic constraints of the study.

METHODS

Study Area

The study was conducted on the Helena National Forest in the Elkhorn Wildlife Management Unit located approximately 16 km southeast of Helena, MT (46°46' N, 111°91' W). The study area is typical of dry mixed coniferous forest, dominated by ponderosa and lodgepole pine with lesser amounts of Douglas fir (*Pseudotsuga menziesii*); the latter two species are typically found on wet north-facing slopes, whereas the former favors dry south-facing slopes. The shrub understory includes common snowberry (*Symphoricarpos albus*), white spirea (S*piraea betulifolia*), common bearberry (*Arctostaphylos uva-ursi*), common juniper (*Juniperus communis*) and Wood's rose (*Rosa woodsii*). Quaking aspen occurs along snow-melt drainages and riparian areas. Under-story shrubs in riparian areas include mountain alder (*Alnus incana* subsp. *tenuifolia*), red osier dogwood (*Cornus sericea*), and Western serviceberry (*Amelanchier alnifolia*).

Four study units were established in 2002-2003 ranging from 1,500 to 1,700 m in elevation and from 135 to 270 ha in area. Originally, this study was part of the USDA Forest Service Birds and Burns Network[2] investigating the effects of prescribed fire strategies to restore wildlife habitat in ponderosa pine forests of the Interior West. Study units consisting of similar forest types, canopy closures, and topography were paired; one unit was planned for treatment (i.e., prescribed fire) and the other was planned as an untreated control (i.e., left unburned). Data were collected from 2003 to 2006, corresponding to years prior to planned treatments. Litigation, however, prevented these treatments from being implemented and consequently, no

[2] USDA Forest Service Rocky Mountain Research Station Birds and Burns Network: http://www.fs.fed.us/rm/wildlife-terrestrial/birds-burns/

data were collected between 2007 and 2008. A mountain pine beetle epidemic began within the study area in 2006 and resulting tree-mortality peaked in 2008 (B. Bentz unpublished). We resumed data collection in 2009 and continued through 2013 on all study units to examine avian population changes in relation to this MPB epidemic.

We recognized two distinct time periods; we considered 2003-2006 to be the pre-epidemic period and 2009-2013 to be post-epidemic. Forest conditions changed dramatically between the pre- and post-epidemic periods. Few *Pinus* spp. snags ≥ 23 cm diameter-at-breast height (measured at 1.37 m above the ground) existed during the pre-epidemic period (6.7 per ha, SE = 0.8, measured 2002-2003) compared to the post-epidemic period (124.2 per ha, SE = 7.6, measured in 2010) (Mosher 2011). The pre-epidemic period typified "green" coniferous forest with many live conifers and few snags (before 2007), whereas the post-epidemic period transitioned to a "red" stage defined by large numbers of *Pinus* spp. with dead needles denoting recent MPB mortality (approx. 2007-2010), and then to a "gray" stage where snags dropped their needles (approx. 2010-2013). Forest conditions in drainages containing aspen woodlands seemingly remained constant throughout the study.

Nest Searching and Monitoring

We conducted nest searches for focal species (ATTW, HAWO, DOWO, NOFL, and RNSA) across all four study units (744 ha total) during all nine years of the study (2003-2006, 2009-2013) (see Dudley and Saab 2003). Every year, two surveys during the breeding season (approximately May 15th to August 1st) were conducted on each study unit along belt transects spaced 200 m apart, which allowed observers to meander 100 m from the transect center in search of focal species and their nests (Figure 1). To aid in detection of focal species (especially

early in the season), we used audio playback (Foxpro Inc., Lewistown, PA, USA), and revisited a site if a detection of a focal adult occurred.

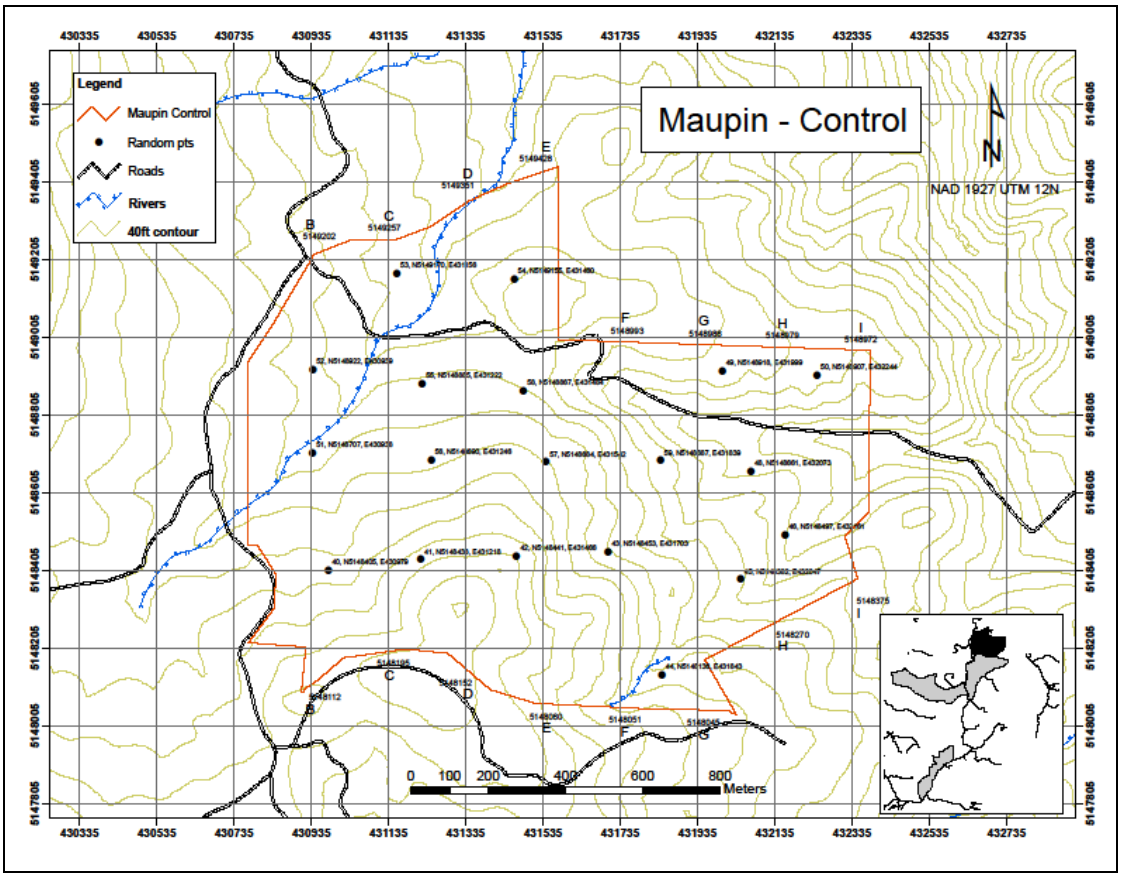

Figure 1: A contour map depicting one of the four study units (Maupin Control) with unit boundaries, non-nest random points (used for point counts and snag surveys), roads, and riparian corridors. Transects (labeled B through I) spaced 200m apart were used for conducting nest surveys of focal species.

Once woodpeckers were located along transects, we used behavioral cues to assess the stage of their nesting cycle. Nesting attempts were indicated directly by observing the excavation of a cavity or copulation of two adults near a suspected cavity. The presence of fresh wood chips under a recently excavated cavity was an indirect indication of a nesting attempt. Both direct and indirect evidence required at least one follow-up visit to determine the nesting

status. Confirmation of a nesting attempt required observation of likely incubation behavior (adults remaining in the cavity for long periods or adults switching positions in and out of the cavity) or direct observation of eggs. Nest contents were observed by using a portable nest camera (Tree Top II System, Sandpiper Technologies, Inc., Manteca, CA; Dudley and Saab 2003, Saab et al. 2007) if the nest cavity was no higher than 15m and the cavity was shaped to allow viewing of the contents. Nest status could also be determined at later stages in the nesting cycle by observations of adults feeding young, or by auditory detections of begging nestlings.

We typically monitored nests every 2 to 5 days, but on rare occasions 7 or more days separated nest visits, until nest fate was determined. Nesting attempts were monitored until at least two 30 minute visits yielded no activity. A successful nest was defined as one that fledged ≥ 1 nestling. Evidence of a successful nest included: 1) observing ≥ 1 nestling fledge from the cavity; 2) adults feeding ≥1 fledgling in close proximity to the nest tree near the expected time of fledging; and 3) visiting a cavity with no activity, but during the previous visit ≥ 1 nestling was observed at an advanced stage (i.e., nestlings begging loudly with their heads out of the cavity, or a nestling visible in the cavity when fed by an adult). If direct viewing of the contents of a cavity was possible, an empty cavity with no remains of nestlings at advanced stages (i.e., flight feathers evident) was evidence to support successful fledging. We defined an unsuccessful nest as a failure to observe nesting behavior after a nest was confirmed (≥ 1 egg) and where no fledging event occurred. Evidence for nest failure included: 1) destruction of the nest cavity or nest tree prior to the expected fledging date; 2) observation of broken eggs, dead nestlings, or a foreign species occupying the cavity; or 3) lack of nesting activity prior to the expected fledging date. When possible, direct observation of the nest contents with the use of a camera was used as supplemental evidence of failure.

Red Squirrel Counts

We randomly selected 76 points placed across all four study units to serve as point centers for conducting red squirrel counts independent of nest locations. Random point centers were placed at least 250 m apart (to consider each point independent) and 200 m from study unit boundaries (Figure 1). RESQ point counts were conducted at all 76 random points three times per season beginning just after the dawn chorus and concluding by 11 am between May 22nd and July 3rd during all nine years of the study. Point count visits consisted of five minute surveys where observers recorded individual and multiple detections of RESQ, along with estimated distance, using both visual and auditory cues. Previous research suggests that red squirrels spend a majority of their time, year round, within 100 m of the focal center of their territory (Lair 1987). We used the maximum number detected, out of three visits, at each random point per year to represent an estimate of predation risk at the nearest nest (i.e., 76 maximum RESQ counts per random point per year).

Remotely Sensed Metrics of MPB Severity

Remotely sensed data were used to quantify MPB epidemic severity at nest-site and home range spatial scales (1 and 314 ha) centered on nest sites, hereafter referred to as the local- and landscape-scales, respectively. We began with year-specific values for spatial indices of MPB severity generated from spatial models for 30x30 m pixels within the study area. We used descriptive statistics for aerial survey data along with spatial models (Crabb 2013) to translate index values to year- and pixel-specific estimates of tree-mortality (i.e., number of *Pinus* spp. per ha killed by MPB). We only calculated pixel-specific values of tree-mortality for years when these severity indices were verified to be informative: 2009-2011. For subsequent

years, we assigned all pixels the average estimated tree-mortality values, hereafter referred to as "annual tree-mortality" (3 and 0 trees killed per ha for 2012 and 2013, respectively), which were insubstantial compared to average estimated values in preceding years (Crabb 2013). For each pixel in each year, we also calculated an estimate of overall tree-mortality, hereafter referred to as "cumulative tree-mortality", by adding together annual tree-mortality estimates for each pixel for years preceding the focal year. This second set of estimates quantified the number of snags that had been generated within each pixel through a given year.

From annual and cumulative tree-mortality estimates, we generated two variables describing the mean estimates within moving windows corresponding to the spatial scales of interest. Thus, we generated four variables describing MPB epidemic severity at two spatial scales centered on each nest: 1) local-scale (1ha) annual tree-mortality; 2) local-scale cumulative tree-mortality; 3) landscape-scale (314ha) annual tree-mortality; and 4) landscape-scale cumulative tree-mortality.

Statistical Methods

Modeling Nest Survival

To address our primary question of interest, we analyzed daily nest survival (DSR) as a function of continuous and categorical covariates using generalized linear models describing daily nest fate (0 = survived; 1 = failed) as independent Bernoulli trials (Dinsmore et al. 2002, Rotella et al. 2004). Specifically, we modeled DSR of a nest on day *i* as a function of covariates (x_{ij}) according to the equation:

$$DSR_i = \frac{\exp(\beta_0 + \sum_{j=1}^{J} \beta_j x_{ij})}{1 + \exp(\beta_0 + \sum_{j=1}^{J} \beta_j x_{ij})}$$

where DSR_i is expressed as a function of J covariates, the slope of the relationship with covariate x_{ij} is β_j, and $\beta_0 + \sum_{j=1}^{J} \beta_j x_{ij}$ describes the log odds of daily survival (Rotella et al. 2004). We used a logit link to relate linear responses to predictor variables on the log odds scale (range: -∞, ∞) with DSR estimates (range: 0, 1) and we used maximum likelihood methods for fitting models (Rotella et al. 2004).

We used program MARK (White and Burnham 1999) to model DSR via the package RMark (Laake 2013) in program R (R Core Team 2013). To construct encounter histories analyzed by program MARK, we compiled the following for each nest: 1) day of the season the nest was first located, 2) last day the nest was observed active, 3) last day the nest was observed, and 4) fate of the nest (0=success, 1=failure) (White and Burnham 1999). When modeling DSR, we included all visits to a nest, and assumed that nest fates were assigned correctly, daily survival rates were homogeneous for any nest on any day with a given set of covariate values, nest survival outcomes on any given day were independent of each other, observation did not influence outcome, and observation of nests was unrelated to their fate (i.e., nests were checked regardless of the perceived outcome). We specified an overall season length in Program MARK as the earliest and latest day-of-season on which nests were observed active across all study years. In this study, May 17 and July 31 were considered the first and last day-of-season (day 1 and day 75) respectively for all species.

We modeled DSR relationships with covariates and then translated these estimates ($\widehat{DSR}$) to estimates of overall nest survival rate ($\widehat{NSR}$) across the entire nesting period using the following equation:

$$\widehat{NSR} = (\widehat{DSR})^d$$

where d represents the number of days necessary for nestlings of a given species to fledge (Table 1). We estimated the variance associated with changing the temporal scale from $\widehat{DSR}$ to $\widehat{NSR}$ using the delta method (Powell 2007):

$$var\left(\widehat{NSR}\right) = d^2 \cdot var\left(\widehat{DSR}\right) \cdot \left(\widehat{DSR}\right)^{(2d-2)}$$

We used $\widehat{NSR}$ to translate $\widehat{DSR}$ to biologically meaningful terms that incorporate differences in length of nesting period between woodpecker species (Table 1). When presenting graphical representations of covariate relationships, we plot $\widehat{NSR}$ relationship in addition to $\widehat{DSR}$ relationships because NSR is often more interpretable. However, this method of converting $\widehat{NSR}$ to $\widehat{DSR}$ ignores time-varying covariates (e.g., temperature, day-of-season) and we advise caution when interpreting graphical representation involving them.

Table 1: Length of nesting periods used to calculate estimates nest survival rate ($\widehat{NSR}$) from estimates of daily survival rate ($\widehat{DSR}$) for five species of woodpecker. Picoides species are shown as a group (*Picoides* spp.) and as individual species. Nesting period refers to the average number of days (d) in the nesting cycle adopted from Dudley and Saab (2003).

Species	Nesting Period (d)
Picoides spp.	42 (3.7)[a]
American three-toed woodpecker (ATTW)	40.5
Hairy woodpecker (HAWO)	46
Downy woodpecker (DOWO)	39
Northern flicker (NOFL)	45.5
Red-naped sapsucker (RNSA)	44

[a]Standard deviation of the average nesting period length for *Picoides* spp.

Covariates Used in Nest Survival Analysis

We modeled DSR relationships of nests with 13 covariates that represented three model sets: 1) non-MPB factors of known importance identified in previous studies of cavity-nesting birds; 2) MPB epidemic conditions; and 3) RESQ relative abundance (hereafter non-MPB, MPB, and RESQ covariates, respectively; Table 2). The non-MPB covariates of daily maximum

temperature (T_{max}) and daily total precipitation were both recorded at the nearest SNOTEL[3] site approximately 14 km SE of the study area (SNOTEL site #893, Tizer basin, MT). We related DSR to precipitation values from the previous day (P_{prev}) to represent the potential lagged-effects of precipitation on food resources. We investigated the possibility that DSR varied with

Table 2: Covariates (by covariate type: non-MPB, MPB, and RESQ) used in models of daily nest survival (DSR) for 5 species of woodpecker. Prediction refers to the hypothesized relationship of the predictor variable (i.e., covariate) on the response variable (i.e., DSR) by species: negative relationship (-), no relationship (0), positive relationship (+), all species (AS), *Picoides* spp. (American three-toed, hairy, and downy woodpeckers; Pic), northern flicker (NF), and red-naped sapsucker (RN).

Covariate Type	Covariate	Prediction	Description
Non-MPB	T_{max}	(-) Pic (+)NF, RN	Maximum daily temperature taken at the nearest SNOTEL[a] station (°C)
	P_{prev}	(0) Pic, NF (-) RN	Previous day's precipitation total taken at the nearest SNOTEL[a] station (mm)
	Day	(+) AS	Linear relationship between DSR and day-of-season
	Day^2	(+) AS	Quadratic relationship between DSR and day-of-season
	Nht	(+) AS	Height of the nest above the ground (m)
	DBH	(+) AS	Diameter-at-breast height of the nest tree (cm)
	Aspen	(-) Pic (+) NF, RN	Nest tree type (0 = *Pinus* spp.; 1= *Populus* spp.)
MPB	MPB_{per}	(+) Pic, NF (0) RN	MPB period (0 = pre-epidemic [2003-2006]; 1= post-epidemic [2009-2013])
	$AM_{1ha, 314ha}$	(+) Pic, NF (0) RN	Estimated annual tree-mortality (*Pinus* spp. per ha) within 1 and 314 ha of the nest
	$CM_{1ha, 314 ha}$	(+) Pic, NF (0) RN	Estimated cumulative tree-mortality (*Pinus* spp. per ha) within 1 and 314 ha of the nest
RESQ	$RESQ_{max}$	(-) AS	Estimated maximum abundance of red squirrels from nearest point count station applied to a nest

[a] SNOTEL site #893, Tizer basin, MT

[3] USDA National Resources Conservation Service (NRCS): http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=893&state=mt

day-of-season and fit the data to a constant nest survival model and then imposed linear and quadratic effects of day-of-season (Day and Day^2). Additionally, we considered three other non-MPB covariates describing nest site characteristics: nest height (Nht), diameter at breast height of the nest tree (DBH), and nest tree genus (Aspen = 1, *Pinus* spp. = 0).

Five covariates described measures of MPB epidemic timing and severity (Table 2). A categorical temporal covariate distinguished between pre- (2003-2006) and post-epidemic (2009-2013) periods (MPB_{per}). We used data compiled by Crabb (2013) representing spatial variation in MPB epidemic severity to derive year-specific GIS layers that estimated the mean annual tree-mortality centered upon nest locations at local (AM_{1ha}) and landscape (AM_{314ha}) scales. We also calculated cumulative tree-mortality estimates centered on nests as the sum of annual tree-mortality estimates leading up to the focal year (CM_{1ha} and CM_{314ha}; where $CM_t = \sum AM_{1,2,\ldots,t}$). We measured tree-mortality in the field, but field and remotely sensed measurements were highly correlated (Pearson's r = 0.65). Additionally, some nests lacked field measurements, so we only used remotely sensed measurements of tree-mortality as covariates.

We considered an index of RESQ abundance as a covariate in DSR models because of the potential importance of nest predation by RESQ, and the negative response by RESQ to the MPB epidemic (Mosher 2011). Specifically, we applied the maximum annual RESQ count ($RESQ_{max}$) recorded at the nearest point count station as an index of local RESQ abundance at a given nest of the same year as the count (average distance of random point to nest = 174 m, sd = 97, range = 0, 588; Table 2).

Model Set Construction and Selection

We constructed candidate DSR models that estimated MPB and RESQ covariate relationships after accounting for non-MPB covariate relationships. We used information-

theoretic model selection to rank candidate models by small-sample corrected Akaike's Information Criteria (AIC_c) and associated Akaike weights (Burnham and Anderson 2002). We evaluated the top competing model(s) within 2 AIC_c units of the highest ranked model. To avoid problems elicited by multicollinearity among predictor variables, we did not include highly correlated covariates ($r \geq 0.65$) in the same model (Neter et al. 1996).

We constructed and selected models of DSR for nests of *Picoides* spp., NOFL, and RNSA (3 separate datasets) in three steps. In step 1, we identified top-performing combinations of non-MPB covariates. We considered additive combinations of these covariates (hereafter the non-MPB model set) excluding combinations with highly correlated covariates ($r \geq 0.6$; Appendices A, B, C, D, E). Specifically, day-of-season was highly correlated with T_{max} (Pearson's $r = 0.69$; Appendix D), so the two were never considered together. Additionally, due to no variation in nest tree genus, we never considered nest tree species (Aspen) in models for RNSA (i.e., all RNSA nests were found in aspen). We screened redundant models by removing those that appeared within 2 AIC_c units of the top model but contained one or more uninformative parameters (further supported by estimated 95% CIs that included zero) from the non-MPB set, and retained qualifying models for use in steps 2 and 3 (Arnold 2010).

In step 2, we constructed models that additively combined MPB covariates with top non-MPB covariate combinations retained in step 1 (hereafter the MPB model-set) excluding any highly correlated pairs (Appendices A, B, C, E) or pairs that measured the same feature at two different spatial scales (i.e., CM_{1ha} and CM_{314ha} or AM_{1ha} and AM_{314ha} were never included in the same model). After identifying the best-fitting additive models, we constructed additional models that included an interaction between T_{max} and MPB_{per} for the *Picoides* spp. only to represent the hypothesis that nests of these species would be adversely affected by higher

maximum daily temperatures due to heat stress from solar exposure in areas of high conifer mortality (Neal et al. 1993, Conway and Martin 2000, Saab et al. 2011). For each additive model that included this pair of covariates, we also considered an equivalent model that included the interaction. We z-scored all interacting covariates (subtracted the mean and divided by the standard deviation) to standardize across differing scales (Schielzeth 2010).

In step 3, we constructed models that additively combined the RESQ covariate with top non-MPB covariates (from step 1), excluding highly correlated pairs (Appendices A, B, C). Red squirrel abundance is not a direct description of MPB conditions, but red squirrels related with MPB period (mean pre-epidemic count=1.74/point; mean post-epidemic count=0.72/point; Welch's $t_{df} = 16.5$, $p < 0.001$) and are a known nest predator. Therefore, the change in red squirrel abundance represents one possible mechanistic factor by which the MPB epidemic could affect nest survival. We did not want to confound RESQ effects with MPB covariate relationships, so we modeled the two separately.

From the MPB and RESQ model sets, we retained models that were within 2 AIC_c units of the top model (lowest AIC_c) for inferring covariate relationships of interest. We used the top model (lowest AIC_c) containing a given covariate for inferring DSR relationships with that covariate. We assessed the statistical support for covariate relationships by assessing the extent to which 95% confidence intervals of parameter estimates overlapped zero.

Nest Density

In addition to analyzing nest survival, we examined nesting densities in relation to the MPB epidemic. We estimated densities of hatched nests only because of their high detectability when occupied by nestlings (Russell et al. 2009). Detection rates for nests of two woodpecker species (hairy and black-backed [*Picoides arcticus*]) were highest during the nestling stages (0.9

[95% CLs = 0.71, 0.95]) and lowest during other stages (Russell et al. 2009). Therefore, we used apparent densities of hatched nests (annual number of hatched nests per 40 ha; hereafter, densities of hatched nests) as an index of nest densities because of their high detectability. We calculated apparent densities annually for *Picoides* spp., NOFL, and RNSA separately and tested for pre- versus post-epidemic differences using Welch's *t*-tests (n = 9 years).

RESULTS

We monitored 196, 52, and 124 nests of *Picoides* spp. (i.e., ATTW, HAWO, and DOWO), northern flicker (NOFL), and red-naped sapsucker (RNSA), respectively, during the nine-year study period (2003-2006 and 2009-2013; Table 3). At these nests we recorded 3479, 1266, and 3566 exposure days, for *Picoides* spp., NOFL, and RNSA, respectively. Nests were found more often during the nestling stage (51%; 190 of 373 nests) compared with those found during egg-laying or incubation stages. We observed a total 67 nest failures, 27 and 40 failures for pre- and post-epidemic periods, respectively. One *Picoides* spp. nest (DOWO) was excluded from the analysis because it was not monitored to completion, resulting in an unknown fate.

Table 3: Number of nests monitored (n), number of failed nests (F), and number of exposure days ($n_{effective}$) for each species (*Picoides* spp. is the sum of ATTW, HAWO and DOWO) grouped by MPB period (pre-MPB = 2003-2006; post-MPB = 2009-2013; Total = both periods combined).

Species	Pre-MPB n, F ($n_{effective}$)	Post-MPB n, F ($n_{effective}$)	Total n, F ($n_{effective}$)
Picoides spp.	39, 11 (748)	157, 24 (2731)	196, 35 (3479)
ATTW	8, 4 (190)	45, 6 (646)	53, 10 (836)
HAWO	19, 6 (361)	58, 14 (1077)	77, 20 (1438)
DOWO	12, 1 (197)	54, 4 (1008)	66, 5 (1205)
NOFL	15, 5 (328)	37, 6 (938)	52, 11 (1266)
RNSA	57, 11 (1616)	67, 10 (1950)	124, 21 (3566)

Summary of DSR Covariate Relationships

On average, we located nests of NOFL earliest in the season (June 7th i.e., day 22 ± 12) followed by RNSA and *Picoides* spp., respectively (June 13th, i.e., day 28 ± 12, and June 17th, i.e., day 32 ± 15, respectively; Table 4). Nests of RNSA were active latest in the season (July 12th, i.e., day 57 ± 10) preceded by *Picoides* spp. and NOFL, respectively (July 5th i.e., day 50 ± 13, and July 1st i.e., day 46 ± 13). Average nest heights were similar among all species, whereas nests of

NOFL were placed in larger diameter (DBH) trees on average (37.7 ± 13.5 cm) than *Picoides* spp. or RNSA (32.0 ± 10.6 cm, and 31.6 ± 7.5 cm, respectively). Nests of *Picoides* spp. and NOFL were located primarily in aspen (61% and 71%, respectively) with fewer nests placed in *Pinus* spp (either lodgepole or ponderosa pine). Nests of RNSA however, were located exclusively in aspen. Average annual and cumulative tree-mortality at local- and landscape-scales were highest surrounding nest sites of *Picoides* spp. (see Table 4). Maximum RESQ counts associated with nest locations were comparable for NOFL and *Picoides* spp. (0.94 ± 0.80, and 0.95 ± 0.81, respectively), and lower for RNSA (0.69 ± 0.66).

Table 4: Summary of covariate values (average, sd), followed by minimum and maximum values (in parentheses) grouped by covariate type used in DSR models for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers), northern flicker (NOFL), and red-naped sapsucker (RNSA) over nine years (2003-2006, 2009-2013) in the Elkhorn Mountains of Montana. "First found" refers to the average day that a nest was found and "Last present" refers to the last day the nest was observed active (day 1 = May 17th; day 76 = July 31st). Values for T_{max} (°C) and P_{prev} (mm) were applied to all nests. Aspen refers to the percent of nests found in aspen trees. Values for MPB_{per} are the proportion of nests found in the post-epidemic period (2009-2013). Refer to Table 2 for other covariate descriptions.

Cov. Type	Cov.	Species		
		Picoides spp.	NOFL	RNSA
	First found	32,15 (1,66)	22,12 (3,52)	28,12 (4,57)
	Last present	50,13 (8,75)	46,13 (8,74)	57,10 (22,75)
Non-MPB	T_{max}	18.5,6.4(0.8,29.8)	-	-
	P_{prev}	025,0.53(0.00,55.3)	-	-
	Nht	9.0,4.3 (2.2,25.3)	8.8, 3.6 (1.6,19.1)	9.1, 3.7 (2.0,19.0)
	DBH	32.0, 10.6 (14.0,70.4)	37.7, 13.5 (17.4,67.5)	31.6, 7.5 (16.4,64.0)
	Aspen	61%	71%	100%
MPB	MPB_{per}	80%	71%	54%
	AM_{1ha}	3.7,7.3 (0.0,34.4)	1.3,3.4 (0.0,18.2)	2.4,6.4 (0.0,42.8)
	AM_{1km}	3.3,6.2 (0.0,22.7)	1.2,2.8 (0.0,16.1)	2.4,5.4 (0.0,22.1)
	CM_{1ha}	49.9,30.8 (0.0,106)	39.4,30.1 (0.0,89.9)	30.1,31.4 (0.0,106)
	CM_{1km}	46.6,24.3 (0.0,71.6)	41.5,27.3 (0.0,70.3)	31.8,29.9 (0.0,67.1)
RESQ	$RESQ_{max}$	0.95,0.81(0.00,4.00)	0.94,0.80 (0.00,3.00)	0.69,0.66 (0.00,4.00)

Statistical Results

DSR of *Picoides* spp. Nests

For *Picoides* spp., we found statistical support for DSR relationships with non-MPB covariates, whereas relationships with MPB or RESQ covariates were not statistically supported. An additive model with maximum daily temperature (T_{max}) and nest tree diameter-at-breast height (DBH) was the top model in the non-MPB model set (step 1 of modeling procedure; Table 5), as well as in the MPB and RESQ sets (steps 2 and 3 of modeling procedure; Table 6). Nest survival was positively related with both T_{max} ($\hat{\beta}$ = 0.07, 95% CLs = 0.00, 0.13) and DBH ($\hat{\beta}$ = 0.04, 95% CLs = 0.00, 0.08) of *Picoides* spp. (Table 7; Figure 2). Although local-scale annual mortality (AM_{1ha}) appears in the second model in the MPB set for *Picoides* spp. (Table 6), the covariate was not statistically supported ($\hat{\beta}$ = 0.03, 95% CLs = -0.04, 0.09; Table 7). MPB period (MPB_{per}) and maximum red squirrel abundance ($RESQ_{max}$) appear in models within 2 ΔAIC_c points of the top model in their respective sets (MPB and RESQ sets), but there was no statistical support for

Table 5: Model selection results for non-MPB candidate models (step 1 of modeling procedure) for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers), northern flicker (NOFL), and red-naped sapsucker (RNSA). K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, and ΔAIC_c = model AIC_c – minimum ΔAIC_c. For complete covariate names and descriptions, see Table 2. Models presented are those within 2 ΔAIC_c units of the minimum ΔAIC_c score (ΔAIC_c for the top model in each set) that do not contain redundant parameters and constant DSR models (no covariates).

Species	Model	K	AIC_c	ΔAIC_c
Picoides spp.	T_{max} + DBH	3	307.57	0.00
	DBH	2	309.46	1.89
	Constant	1	313.15	5.57
NOFL	Constant	1	99.84	0.00
RNSA	Nht + DBH	3	201.94	0.00
	Constant	1	212.29	10.35

either covariate (MPBper $\hat{\beta}$ = 0.21, 95% Cls = -0.55, 0.97; $RESQ_{max}$ $\hat{\beta}$ = 0.18, 95%CLs = -0.22, 0.59; Table 7). As a result, estimates of DSR differed little with respect to MPB period or increased RESQ abundance for *Picoides* spp. (Tables 8, 9).

Table 6: Model selection results for MPB and RESQ candidate models (steps 2 and 3) for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers). K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, and ΔAIC_c = model AIC_c – minimum ΔAIC_c. For complete covariate names and descriptions, see Table 2. Models presented are those within 2 ΔAIC_c units of the minimum ΔAIC_c score (ΔAIC_c for the top model in each set) and constant DSR models (no covariates).

Model set	Model rank	Model	K	AIC_c	ΔAIC_c
MPB	Pic-A1	T_{max} + DBH	3	307.57	0.00
	Pic-A2	T_{max} + DBH + AM_{314ha}	4	308.84	1.27
	Pic-A3	T_{max} + DBH + MPB_{per}	4	309.28	1.71
	Pic-A4	T_{max} + DBH + CM_{1ha}	4	309.40	1.83
	Pic-A5	DBH	2	309.46	1.89
	-	Constant	1	313.15	5.57
RESQ	Pic-B1	T_{max} + DBH	3	307.57	0.00
	Pic-B2	T_{max} + DBH + $RESQ_{max}$	4	308.76	1.19
	Pic-B3	DBH	2	309.46	1.89
	-	Constant	1	313.15	5.57

Table 7: Estimates and 95% confidence limits (LCL, UCL) for parameters in top DSR models for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers). Source models are indicated by their model rank in model selection results for *Picoides* spp. (see Table 6). Covariates with 95% CLs that do not include zero are in bold.

Parameter	Source Model			
	Pic-A1	Pic-A2	Pic-A3	Pic-B2
Intercept	2.21 (0.72, 3.70)	2.14 (0.66, 3.63)	2.19 (0.71, 3.67)	1.88 (0.22, 3.55)
T_{max}	**0.07 (0.00, 0.13)**	**0.06 (0.00, 0.13)**	**0.06 (0.00, 0.13)**	**0.07 (0.01, 0.13)**
DBH	**0.04 (0.00, 0.08)**	**0.04 (0.00, 0.08)**	**0.04 (0.00, 0.08)**	**0.04 (0.00, 0.08)**
AM_{314ha}		0.03 (-0.04, 0.09)	-	-
MPB_{per}		-	0.21 (-0.55, 0.97)	-
$RESQ_{max}$		-	-	0.18 (-0.22, 0.59)

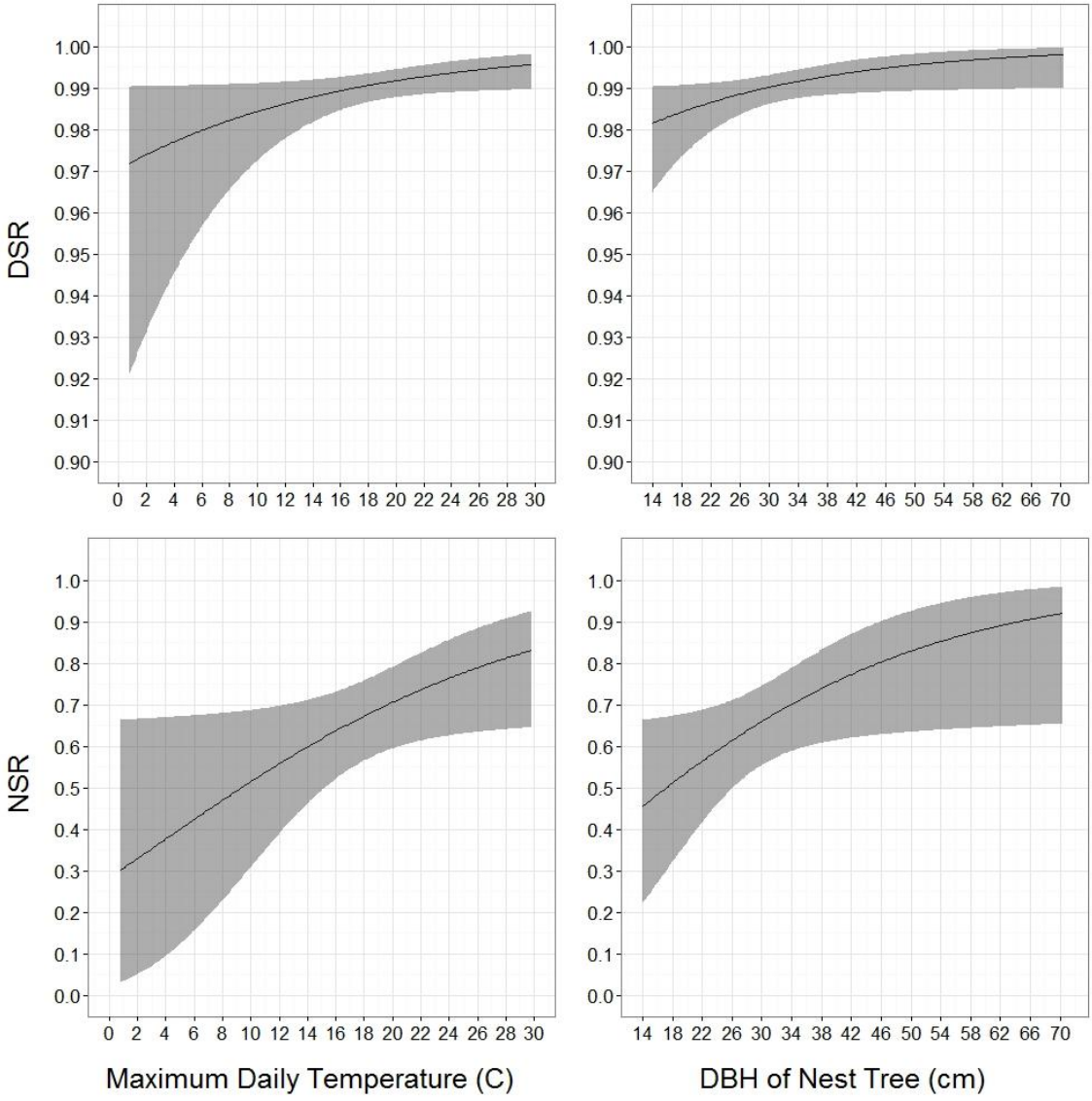

Figure 2: Predicted nest survival rates (daily survival rates [DSR; top row] and nest survival rates [NSR; bottom row]) from the top model for *Picoides* spp. (Pic-A1; Table 6) depicting statistically supported covariate relationships (maximum daily temperature [T_{max}], and DBH of the nest tree [DBH]; Table 7). Estimates are represented by solid black lines with 95% confidence bands (shaded areas). Nest survival estimates (both DSR and NSR) are plotted across the range of observed values for a given covariate (x-axis) with other covariates appearing in models fixed at mean values (for covariate descriptive statistics, see Table 4).

Table 8: Estimates of daily survival rate (DSR) and nest survival rate (NSR) and 95% confidence limits (LCL, UCL) for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers), northern flicker (NOFL), and red-naped sapsucker (RNSA) for the pre- (2003-2006) and post- (2009- 2013) MPB periods. Estimates are from top models containing the MPB_{per} covariate with other covariates in the models held at mean values (see table 4 for covariate summaries).

		pre-MPB	Post-MPB
Picoides spp.[a]	DSR	0.989 (0.979, 0.995)	0.991 (0.987, 0.994)
	NSR	0.636 (0.411, 0.795)	0.693 (0.576, 0.784)
NOFL[b]	DSR	0.985 (0.965, 0.994)	0.994 (0.985, .0997)
	NSR	0.506 (0.196, 0.754)	0.748 (0.498, 0.887)
RNSA[c]	DSR	0.994 (0.989, 0.997)	0.997 (0.993, 0.999)
	NSR	0.789 (0.621, 0.879)	0.874 (0.737, 0.937)

[a] *Picoides* spp. model = DSR ~ T_{max} + DBH + MPB_{per} (see Tables 6 and 7)
[b] NOFL model = DSR ~ MPB_{per} (see Tables 10 and 11)
[c] RNSA model = DSR ~ Nht + DBH + MPB_{per} (model $\Delta AIC_c > 2$, i.e., does not appear in Tables 10 or 11)

Table 9: Estimates of daily survival rate (DSR) and nest survival rate (NSR) and 95% confidence limits (LCL, UCL) for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers), northern flicker (NOFL), and red-naped sapsucker (RNSA) for fixed values of maximum red squirrel abundance ($RESQ_{max}$) of 0 and 2. Estimates are from top models containing the $RESQ_{max}$ covariate with other covariates in the models held at mean values (see table 4 for covariate summaries).

		$RESQ_{max}$ = 0	$RESQ_{max}$ = 2
Picoides spp.[a]	DSR	0.989 (0.982, 0.994)	0.992 (0.987, 0.996)
	NSR	0.634 (0.470, 0.760)	0.730 (0.565, 0.840)
NOFL[b]	DSR	0.995 (0.985, 0.998)	0.988 (0.965, 0.996)
	NSR	0.783 (0.498, 0.918)	0.566 (0.199, 0.820)
RNSA[c]	DSR	0.997 (0.992, 0.999)	0.995 (0.991, 0.997)
	NSR	0.870 (0.700, 0.942)	0.812 (0.667, 0.889)

[a] *Picoides* spp. model = DSR ~ T_{max} + DBH + $RESQ_{max}$ (Tables 6 and 7)
[b] NOFL model = DSR ~ $RESQ_{max}$ (Tables 10 and 11)
[c] RNSA model = DSR ~ Nht + DBH + $RESQ_{max}$ (Tables 12 and 13)

DSR of NOFL Nests

We found little evidence for any covariate relationships with nest survival of NOFL (steps 1, 2, and 3 of modeling procedure). A model of constant DSR was the highest ranked

model in the non-MPB, MPB, and RESQ model sets (Tables 5, 10, 11). This model estimated DSR to be 0.9914 (95% CLs = 0.9846, 0.9952), which translates into a NSR of 0.6756 (95% CLs = 0.5191, 0.8322). Single variable nest survival models containing MPB_{per} and $RESQ_{max}$ were the second ranked models in the MPB and RESQ model sets, respectively (Table 10), however, no clear statistical support was found for either covariate (MPBper $\hat{\beta}$ = 0.86, 95% CLs = -0.34, 2.05; $RESQ_{max}$ $\hat{\beta}$ = -0.43, 95%CLs = -1.11, 0.26; Table 11). Differences in nest survival estimates for NOFL with respect to epidemic period (pre and post) and varying red squirrel were not statistically significant (Tables 8, 9).

Table 10: Model selection results for MPB and RESQ candidate models (steps 2 and 3) for northern flicker (NOFL). K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, and ΔAIC_c = model AIC_c – minimum ΔAIC_c. For complete covariate names and descriptions, see Table 2. Models presented are those within 2 ΔAIC_c units of the minimum ΔAIC_c score (ΔAIC_c for the top model in each set).

Model Set	Model rank	Model	K	AIC_c	ΔAIC_c
MPB	NOFL-A1	Constant	1	99.84	0.00
	NOFL-A2	MPB_{per}	2	99.96	0.12
	NOFL-A3	CM_{314ha}	2	100.25	0.41
	NOFL-A4	AM_{314ha}	2	101.08	1.24
	NOFL-A5	CM_{1ha}	2	101.44	1.60
	NOFL-A6	MPB_{per} + AM_{314ha}	3	101.70	1.86
	NOFL-A7	AM_{1ha}	2	101.78	1.94
RESQ	NOFL-B1	Constant	1	99.84	0.00
	NOFL-B2	$RESQ_{max}$	2	101.43	0.59

Table 11: Estimates and 95% confidence limits (LCL, UCL) for parameters in top DSR models for Northen flicker (NOFL). Source models are indicated by their model rank in model selection results for NOFL (see Table 8).

Parameter	Source Model		
	NOFL-A1	NOFL-A2	NOFL-B2
Intercept	4.75 (4.16, 5.34)	4.20 (3.31, 5.08)	5.23 (4.17, 6.28)
MPB_{per}	-	0.86 (-0.34, 2.05)	-
$RESQ_{max}$	-	-	-0.43 (-1.11, 0.26)

DSR of RNSA Nests

For nests of RNSA, we found evidence of DSR relationships with non-MPB and MPB variables (Tables 5, 12). Nest tree diameter (DBH) and nest height (Nht) appeared in all models within 2 ΔAIC_c units of top models in both MPB and RESQ sets (Tables 5, 12). Nest survival increased with increasing Nht and decreased with increasing DBH (Nht $\hat{\beta}$ = 0.26, 95% CLs = 0.09, 0.42; DBH $\hat{\beta}$ = -0.13, 95%CLs = -0.20, -0.06; Table 13; Table 13, Figure 3). Nest survival for RNSA also increased with local-scale cumulative tree-mortality (CM_{1ha} $\hat{\beta}$ = 0.02, 95% CLs = 0.00, 0.03; Table 13; Figure 3). Although $RESQ_{max}$ appeared within 2 ΔAIC_c units of the top model in the

Table 12: Model selection results for MPB and RESQ candidate models (steps 2 and 3) for red-naped sapsucker (RNSA). K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, and ΔAIC_c = model AIC_c – minimum ΔAIC_c. For complete covariate names and descriptions, see Table 2. Models presented are those within 2 ΔAIC_c units of the minimum ΔAIC_c score (ΔAIC_c for the top model in each set) and constant DSR models (no covariates).

Model Set	Model rank	Model	K	AIC_c	ΔAIC_c
MPB	RNSA-A1	Nht + DBH + CM_{1ha}	4	199.71	0.00
	RNSA-A2	Nht + DBH + CM_{1ha} + AM_{1ha}	5	201.55	1.84
	RNSA-A3	Nht + DBH + CM_{1ha} + AM_{314ha}	5	201.69	1.97
	-	Constant	1	212.29	12.58
RESQ	RNSA-B1	Nht + DBH	3	201.94	0.00
	RNSA-B2	Nht + DBH + $RESQ_{max}$	4	203.32	1.38
	-	Constant	1	212.29	10.35

Table 13: Estimates and 95% confidence limits (LCL, UCL) for parameters in top DSR models for red-naped sapsucker (RNSA). Source models are indicated by their model rank in model selection results for RNSA (see Table 10). Covariates with 95% Cis that do not include zero are in bold.

Parameter	Source Model	
	RNSA-A1	RNSA-B2
Intercept	6.94 (5.11, 8.77)	7.48 (5.22, 9.74)
Nht	**0.26 (0.09, 0.42)**	**0.23 (0.08, 0.38)**
DBH	**-0.13 (-0.20, -0.06)**	**-0.122 (-0.19, -0.05)**
CM_{1ha}	**0.02 (0.00, 0.03)**	
MPB_{per}	-	-
$RESQ_{max}$	-	-0.20 (-0.70, 0.29)

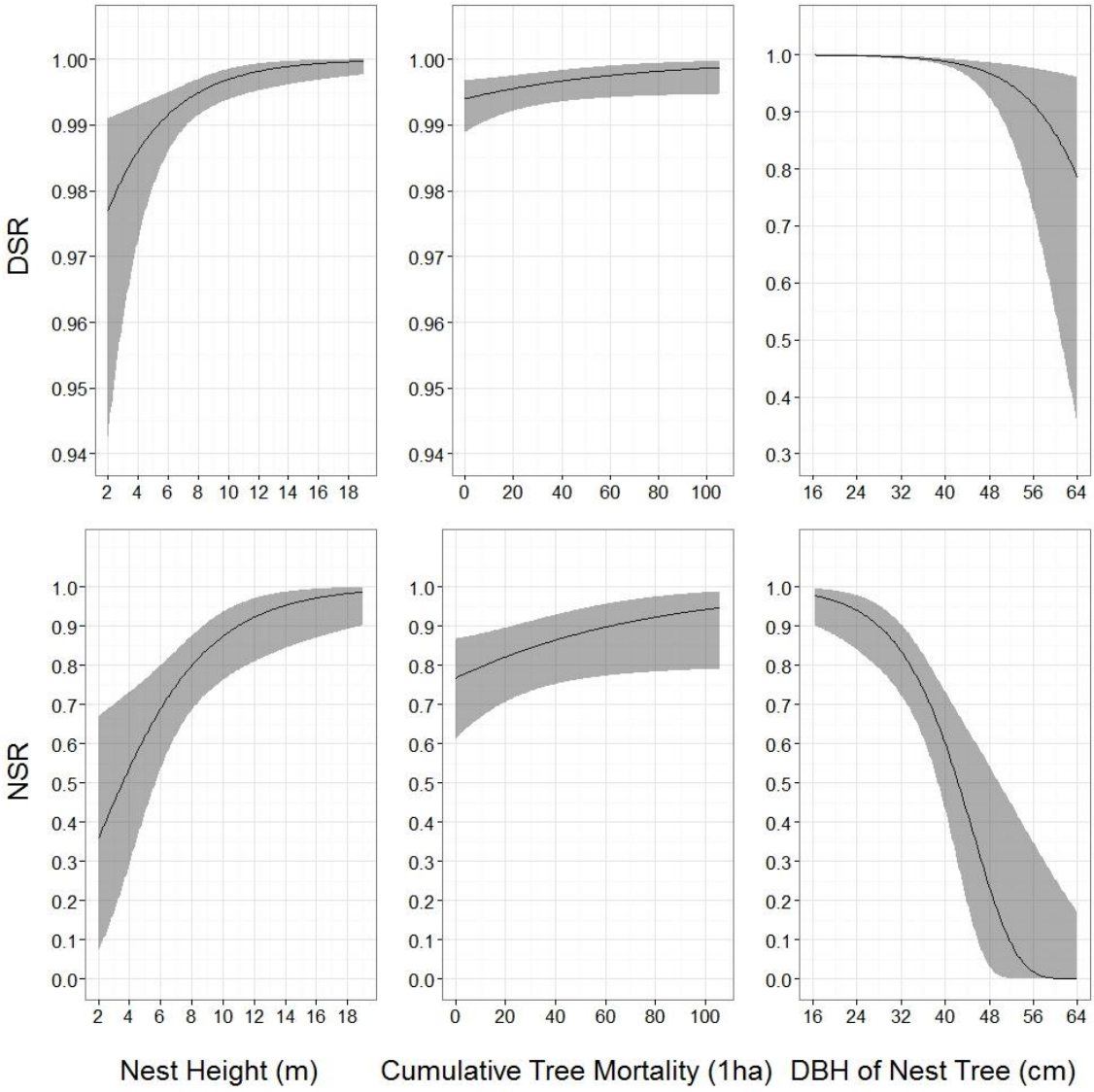

Figure 3: Predicted nest survival rates (daily survival rates [DSR; top row] and nest survival rates [NSR; bottom row]) from the top model in the MPB set for red-naped sapsucker (RNSA-A1; Table 12) depicting statistically supported covariate relationships (nest height [Nht], cumulative tree-mortality at 1 ha [CM_{1ha}], and DBH of nest tree [DBH]). Estimates are represented by solid black lines with 95% confidence bands (shaded areas). Nest survival estimates (both DSR and NSR) are plotted across the range of observed values for a given covariate (x-axis) with other covariates appearing in models fixed at mean values (for covariate descriptive statistics, see Table 4).

RESQ set, it was not statistically supported ($RESQ_{max}$ $\hat{\beta}$ = -0.20, 95% CLs = -0.70, 0.29), resulting in non-significant differences in nest survival estimates for varying maximum RESQ abundances (Table 9). Epidemic period was not statistically supported in the MPB set for RNSA, and period-respective estimates of nest survival from the highest ranked model with MPB_{per} did not differ significantly (Table 8).

Densities of Hatched Nests

We recorded 189, 48, and 118 hatched nests throughout the study period for *Picoides* spp., NOFL, and RNSA, respectively (Appendix F). Of these, 151, 35, and 63 were monitored during the post-epidemic period (*Picoides* spp., NOFL, and RNSA, respectively). We found support for a statistically significant difference in period-respective densities of hatched nests for *Picoides* spp. ($t_{4.4}$ = -3.73, p = 0.02; Fig. 4). The mean number hatched nests of *Picoides* spp. during the pre-epidemic period was 9.5 per year (SD = 2.5), whereas, the mean post-epidemic was 30.2 (SD = 12.1). The 95% confidence interval of the difference between the mean number of hatched nests pre- and post-epidemic is between 5.9 and 35.1 hatched nests. Densities of hatched nests for NOFL also tended to be higher after the epidemic (mean pre-epidemic = 3.3 per year [SD = 1.3]; mean post-epidemic = 7.0 per year [SD = 4.9]), although this difference was not statistically significant ($t_{4.6}$ = -1.63, p = 0.17). Densities of hatched nests for RNSA did not differ notably between the periods (mean pre-epidemic = 13.8 per year [SD = 4.0]; mean post-epidemic = 12.6 per year [SD = 2.9]; $t_{5.3}$ = -0.48, p = 0.65).

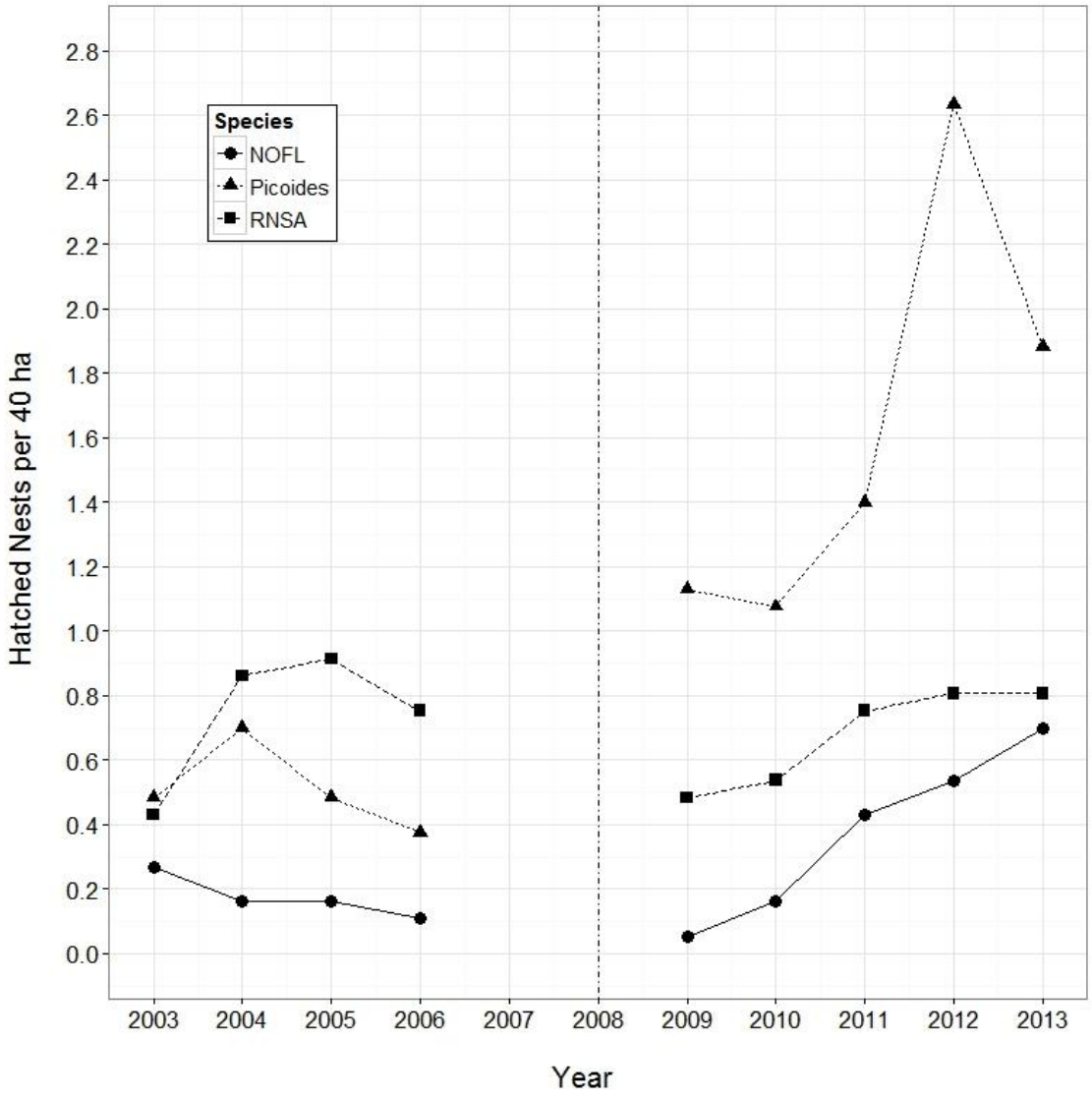

Figure 4: Apparent densities of hatched nests of woodpeckers during a nine-year study in the Elkhorn Mountain of Montana. NOFL = northern flicker; Picoides = *Picoides* spp. (American three-toed, hairy, and downy woodpeckers); and RNSA = red-naped sapsucker. The dashed vertical line represents the peak of the beetle-induced tree-mortality. Densities are represented as hatched nests per 40 ha per year.

DISCUSSION

Although we did not find any statistically supported relationships between nest survival and variables characterizing the MPB epidemic for *Picoides* spp., there was a clear positive numerical response to the outbreak by this group. Generally, we found greater support for DSR relationships with previously documented variables known to affect woodpecker nest survival (i.e., nest tree DBH, nest tree height, and maximum daily temperature). Surprisingly, RNSA was the only species that demonstrated a clear DSR relationship with any covariates related to the MPB epidemic (local-scale cumulative tree mortality).

Nest Survival

We found no clear statistical support for increases in DSR relative to the MPB period despite our predictions of increased nest survival for *Picoides* spp. as a result of the resource pulse brought about by the MPB epidemic (i.e., beetles and nesting substrate). Sample size, however, could have affected our estimates, especially during the pre-epidemic period when nest numbers were lower. The lack of clear DSR relationships with epidemic period corroborates with previous findings from a study in British Columbia, where researchers failed to detect differences in mean fecundity measures (i.e., clutch size and number of nestlings fledged) for any of the three *Picoides* species in response to a large MPB epidemic (Edworthy et al. 2011).

We compared estimates of nest survival of *Picoides* spp. from studies investigating various disturbance types because no published studies report on nest survival in relation to a MPB epidemic. In relatively undisturbed ponderosa pine forests, estimates of HAWO nest success vary; 0.74 (no estimate of precision given) in Arizona (Martin and Li 1992), 0.48 (no

estimate of precision given) in central Idaho (Saab et al. 2005), and 0.61 (95% CLs = 0.38, 0.78) during the pre-epidemic period in our study. Differences among nest survival estimates likely represent variation in resource availability inherent in coniferous forests without recent natural disturbances. In another Idaho study, estimated nest survival for HAWO within 4 years after wildfire (i.e., disturbance conditions similar to our post-epidemic period) was 0.85 (95% CLs = 0.71, 0.93; Saab et al. 2007), which is higher than our point estimate of 0.67 (95% CLs = 0.55, 0.77) from the post-epidemic period. These estimates of nest survival are generally higher than estimates in forests without recent disturbance, highlighting the potential importance of fire and beetle disturbances to HAWO reproductive success.

We hypothesized that DSR would have a positive relationship with epidemic severity surrounding *Picoides* spp. nests, due to the resource pulse available from MPB-killed trees. More specifically, we expected the benefits of nest placement in these high snag areas (i.e., increased forage availability in close proximity to nests) to outweigh the costs of potential increased maximum daily temperatures in denuded forests. Nevertheless, we did not find evidence of an association with tree mortality at the local- or landscape-scale for the *Picoides* spp. We did, however, find that nest locations of these *Picoides* spp. were situated among areas of higher MPB-killed trees compared with NOFL and RNSA (Table 4). These results could be explained by the benefits to *Picoides* spp. being manifested through population demographic parameters other than nest survival in areas of high tree-mortality (e.g., nest densities or juvenile survival). The lack of association between DSR and cumulative tree-mortality might result from inadequate estimates of remotely-sensed snag densities. Cumulative tree-mortality is made up of a combination of three different classifications of snags: 1) annual tree-mortality (i.e., trees recently killed by MPB); 2) standing snags in various stages of decay (e.g., needles

lost, broken top, etc.); and 3) snags that have fallen to the ground (i.e., logs). Estimates of cumulative tree-mortality in early post-epidemic years (i.e., 2009-2010) are generally lower compared with estimates from later years (i.e., 2011-2013) and likely include larger proportions of trees recently killed by MPB (i.e., snags) and smaller proportions of logs. Although estimates of cumulative tree-mortality in later years are higher, this may not accurately represent the food resources available to *Picoides* spp. (i.e., adult and larval MPB). Further breakdown of cumulative tree-mortality into year-specific estimates of standing snags and logs using techniques such as Lidar may result in clearer relationships between DSR and epidemic severity (Bergen et al. 2007).

We found evidence in support of our hypothesis of a positive DSR relationship with DBH for *Picoides* spp. We expected nests to be excavated in larger DBH trees for protection against temperature extremes and predators. Generally, as DBH of the cavity tree increases, the potential diameter of the tree at cavity height also increases, allowing birds to excavate nest cavities with thicker walls (Wiebe 2001). Thicker diameter nest trees likely provide better insulating properties to nests placed within them and act to buffer eggs and nestlings from temperature extremes (Amat-Valero et al. 2014). In addition to the thermal regulation of larger DBH trees, nests placed in larger *Pinus* spp. likely provide substrate that is more structurally sound compared to aspen which is softer and prone to heartwood rot fungus (Basham 1958). We observed 39% of *Picoides* spp. nests in *Pinus* spp. during all years of the study (5% and 48% pre- and post-epidemic, respectively). For a group comprised of strong excavators, placement of nests in harder nest substrate (e.g., *Pinus* spp.) with the potential for thicker cavity walls (i.e., larger DBH) likely provided better protection from predators, such as American black bear,

which have been reported to depredate nests of cavity-nesting birds (Walters and Miller 2001, Paclík et al. 2009, Tozer et al. 2009).

We found a positive association between maximum daily temperature and DSR for *Picoides* spp., which was contrary to our hypothesis. We predicted that nests placed amid high densities of MPB-killed trees, such as those of *Picoides* spp., would be subject to higher maximum daily temperature values due to the loss of canopy closure as needles died and as snags fell. Previous research in western Idaho investigating post-wildfire effects on nest survival identified a negative relationship between maximum daily temperature and DSR for the open-forest nesting Lewis's woodpecker (*Melanerpes lewis*; Saab et al. 2011). Average maximum daily temperatures during the nesting period in the western Idaho study were higher than those observed in our western Montana study area (23.6 °C, range = 11.9, 39.7; and 18.5 °C, range = 0.8, 29.8 in Idaho and Montana, respectively). This suggests that observed maximum temperatures during the breeding season in our study area were not warm enough to create adverse conditions for heat sensitive eggs and nestlings. Moreover, due to the host-specific nature of beetle epidemics, Douglas-fir and aspen were largely unaffected in Montana, whereas, most of the forest canopy was lost after stand-replacement fires in Idaho. Our study area in Montana might have experienced a cooler microclimate post-disturbance than the Idaho study because of a greater retention of non-host specific canopy closure. Additionally, the Montana study area may have been subject to colder temperatures and early season storms (bringing rain and snow) that may have subjected nestlings to hypothermia (Marcel et al. 2003), as well as creating damp nest conditions that could harbor ectoparasites detrimental to nestling development (cf. Merino and Potti 1996, but see Heeb et al. 2000). When temperatures are

low, nestlings must increase their metabolism to maintain thermoregulation at the tradeoff of growth, in turn, possibly lowering nest survival (Wiebe 2001, Marcel et al. 2003).

We found little evidence of association between DSR and any variables for NOFL. A model of constant DSR was ranked highest in both the MPB and RESQ sets, suggesting that our covariates did little to describe the variation in nest survival for this species. Saab et al. (2011) also reported model selection uncertainty when investigating DSR relationships with several abiotic and biotic covariates for NOFL nests in relation to post-wildfire salvage logging in western Idaho. Similarly, Wiebe (2001) found no association between measures of fecundity for NOFL and several temperature, nest, and nest-tree variables in a study conducted in British Columbia. Another study in British Columbia found a similar lack of relationship between measures of fecundity and a MPB epidemic (Edworthy et al. 2011). This consistent lack of associations with measures of reproductive effort in NOFL might be further evidence in support of this species as a generalist due to its ability to inhabit a wide range of habitat conditions (Wiebe and Moore 2008). This outcome might also suggest that researchers have yet to identify variables important to NOFL reproductive success.

Unexpectedly, we found support for a positive relationship between DSR of RNSA nests and cumulative tree-mortality at the local-scale (i.e., 1 ha). We predicted that food resources and nesting substrate would remain relatively consistent throughout the MPB epidemic for this aspen-nesting species. While we do not have a good explanation for this finding, it could be related to a potential change of the predator community in aspen woodlands resulting from the MPB epidemic. More specifically, this relates to nests placed in aspen that are surrounded by higher numbers of coniferous snags in the surrounding 1 ha area. Perhaps nests in aspen with high conifer mortality surrounding them reduce the effectiveness of predators due to lower

canopy cover that would otherwise act to conceal their approach and subsequent detection by adults at the nest.

DSR for RNSA was relatively similar pre- and post-epidemic, supporting our hypothesis of no change in nest survival in relation to the epidemic. Accordingly, Edworthy et al. (2011) found no change in number of eggs laid and number of nestlings fledged for RNSA as a result of a MPB epidemic. Although few studies have quantified RNSA nest survival in forests with no recent disturbance, our relatively high estimate of 0.79 (95% CLs = 0.62, 0.88) is similar to estimates from a study in forests of central Arizona (1.00; no estimates of precision; Martin and Li 1992). Further, these estimates during the pre-epidemic period were generally higher than DSR estimates for *Picoides* spp. and NOFL (Table 8). This tendency may be explained by higher abundance and the stability of preferred food resources (i.e., sap and a diversity of arthropods) for RNSA, resulting in higher nest survival, compared with those preferred by NOFL and *Picoides* spp. (i.e., ants and adult and larval beetles, respectively) in green forests with lower snag and log densities.

We found support for a negative relationship between nest survival and DBH of RNSA nest trees, contrary to our hypothesis. Differences in the risk of nest predation between aspen woodlands and coniferous forest may explain this opposite DBH relationship compared with *Picoides* spp. The negative relationship could represent a tradeoff between nest placement and predation in aspen woodlands. RNSA are reported to preferentially place their nests in trees infected with heartwood rot fungus (*Phellinus tremulae*), which softens the heartwood and presumably allows for easier cavity excavation by this relatively “weak” cavity-excavating species (Losin et al. 2006). Additionally, stand age in which a tree is found is strongly positively correlated with the proportion of aspen trees with heartwood rot fungus (Basham 1958). RNSA

nest placement often tracks the upward movement of heartwood rot in subsequent years (Daily 1993). This often results in more cavities located in larger (i.e., older) aspen trees. Ground-based predators that hunt primarily by visual cues might remember where nests have been placed from one year to the next, thus, increasing their search efficiency (Tozer et al. 2009). Black bears have been implicated in sapsucker nest depredations in many studies (Deweese and Pillmore 1972, Franzreb and Higgins 1975, DeGraaf 1995, Hannon and Cotterill 1998, Walters and Miller 2001, Tozer et al. 2009). Preferential selection by predators, such as black bears, for larger DBH aspen with the potential for many cavities would maximize the likelihood of finding occupied cavities in order to offset the energetic cost associated with tree ascension. This also may explain the tendency for larger DBH aspen in contiguous groves in our study area to be scarred with claw marks indicating previous tree ascensions by black bears (Dresser pers. obs.). Additionally, RNSA nests placed in smaller DBH trees may be more difficult for large predators to climb, resulting in increased nest survival.

We found evidence of a positive relationship between DSR and nest height for RNSA nests, in accordance with our hypothesis. Higher nests were expected to be more difficult to access and detect by ground-based predators (Best and Stauffer 1980, Nilsson 1984, Li and Martin 1991, Fisher and Wiebe 2006, Saab et al. 2011). Perhaps the relationships that we have identified between RNSA nest survival and nest tree characteristics (i.e., DBH and nest height) in aspen woodlands may further demonstrate the important role that nest site selection plays in mitigating the risk of nest predation.

No statistically supported relationships were found between DSR and estimated maximum red squirrel abundance for any of the species investigated. Our assumptions regarding localized RESQ movements (e.g., a 100 m radius) may have been too restrictive. If

RESQs do have larger home ranges, our method of applying the maximum count from the nearest point count to the nest may not have been adequate in representing RESQ nest depredation risk. Also, RESQ predation in our study area may not have been as strong of a driver of nest survival compared with other studies (e.g., Tewksbury et al. 1998).

Densities of Hatched Nests

We found strong statistical support for our hypothesis of higher nest densities post-epidemic for the *Picoides* spp. Nest densities appeared to increase annually following the epidemic and peaked four years after the height of beetle-induced tree-mortality (2009-2012). This was likely due to the pulse of food resources (i.e., adult and larval MPB) available to *Picoides* spp. Data collected during 2010-2012 from insect traps targeting beetles revealed in 2011 a relatively large proportion of Curculionidae; the insect family containing MPB and other bark beetles (Bentz unpubl. 2014). The large proportion of Curculionidae may have influenced the peak of *Picoides* spp. nest densities in 2012. Moreover, proportions of wood-boring beetles (family Cerambicidae) were relatively consistent during all years of trapping, and are known to be an important food resource (larval stages) for *Picoides* spp. (Leonard 2001, Jackson and Ouellet 2002, Jackson et al. 2002).

Other explanations for short-term post-epidemic increases in nest densities of *Picoides* spp. might include increased immigration rates and reduced distance of natal dispersal. Generally, resources are not uniformly distributed within a species range, resulting in the tendency for higher numbers of individuals to be found in areas with greater resource abundance (e.g., source populations; Runge et al. 2006). Creation of source populations is strongly influenced by the extent of both immigration and natal dispersal (resulting from high

juvenile survival) and dependent on ecological factors such as food availability (Weatherhead and Forbes 1994, Runge et al. 2006).

Of 189 *Picoides* spp. nests, 27% of hatched nests were ATTW, 39% HAWO, and 34% DOWO (Appendix F). We found substantially more nests on an annual basis during the post-epidemic period for each species in the *Picoides* spp. group with 86% of ATTW nests, 74% of HAWO nests, and 81% of DOWO nests found during years 2009-2013 (151 nests total). The high percentage of nests found during the post-epidemic period is especially relevant for ATTW, whose life history traits place it in closest association with beetle disturbance of the three *Picoides* spp. studied (Leonard 2001). During 2012, DOWO represented the majority (51%) of hatched nests for *Picoides* spp. The unexpected peak in DOWO nesting numbers could have been in response to high levels of Western spruce budworm (*Choristoneura occidentalis*), a defoliating agent of Douglas-fir in western North America, observed during the 2012 season (ADS[4] 2012, Dresser pers. obs.). Adult DOWOs have been reported to feed spruce budworm caterpillars to nestlings during years with high concentrations (Jackson and Ouellet 2002).

Few studies have investigated the abundance of cavity-nesting birds in relation to MPB epidemics (Saab et al. 2014). In British Columbia, Martin et al. (2006) found positive trends in mean density of nests for all species in the *Picoides* spp. group. They found that nest densities of *Picoides* spp. increased significantly in the two years following the peak of the beetle-induced tree-mortality in 2003, and continued to increase reaching a maximum approximately 4 years after the height of outbreak conditions (Martin et al. 2006, Edworthy et al. 2011). Likewise, *Picoides* spp. nest densities in our Montana study peaked in 2012 corroborating with the time period for the trend observed in the British Columbia study (i.e., 4 years after the peak beetle-

[4] USDA Forest Service Aerial Detection Survey (ADS) 2012
http://www.fs.usda.gov/detail/r1/forest-grasslandhealth/?cid=stelprdb5285985

induced mortality). Although the dominant tree species were different between the two studies (ponderosa vs lodgepole pine, respectively), similarities in forest successional stages following the epidemic may have resulted in comparable progressions of bark- and wood-boring beetle communities and subsequent temporal changes of *Picoides* spp. nest densities (Edworthy et al. 2011, Mosher 2011, Bentz unpubl. 2014).

Consistent numbers of wood-boring beetles and increased availability of foraging substrate (i.e., decayed snags and logs) could have influenced the positive trend of NOFL nesting densities with epidemic period. Edworthy et al. (2011) also found general increases in NOFL nests with time since the peak of beetle-caused tree-mortality, similar to our findings. This result warrants further study, but may suggest that this species continues to find suitable habitat conditions in later post-epidemic years (i.e., > 5 years).

Expectedly, we found no association between RNSA nest densities and MPB epidemic conditions. The relatively stable condition of aspen woodlands during all years of our study is a likely explanation. The consistency of RNSA nest densities, regardless of MPB period, suggests that our study area supported maximum nest densities during all years of the study.

Scope and Limitations

We were fortunate to have both pre- and post-epidemic data from our study area. This allowed us to investigate demographic relationships of woodpeckers in relation to MPB disturbance while removing the possibility of changes in those relationships being due to differences among geographic areas.

Samples sizes for nests of some species were low during the pre-epidemic period, although this was not due to our sampling effort. The 51 ATTW nests that we found during our

9-year study is similar to the 61 nests found over a 13-year study in British Columbia (Edworthy et al. 2011). This illustrates the difficulty inherent in nesting studies focused on disturbance specialist species, such as ATTW.

Our study evaluated both MPB and non-MPB variables affecting woodpecker nest survival within 5 years of the peak of beetle-caused tree-mortality. This is a relatively short time frame from which to make inferences, as habitat conditions are expected to change substantially 6 years after the peak in tree-mortality, particularly with increasing deadfall and understory shrub growth (Stone 1995, Page and Jenkins 2007). Beginning with those ecological changes, we expect more variation in woodpecker population demographics than our results.

Uncertainty in nest fates (< 15% of nests) based on lack of critical observations, may have had an influence on our results. As such, approaches that address uncertain nest fates, such as those described by Manolis et al. (2000) or Weidinger (2007), may provide a better method for analyzing survival of nests with uncertain nest fates.

Management Implications

Climate models predicting increasing temperatures in future years have been used to demonstrate risks posed to forests by increased periodicity and magnitude of beetle epidemics (Logan and Powell 2001, Kurz et al. 2008, Bentz et al. 2010, Sambaraju et al. 2012). The opportunities for salvage logging in post-disturbance forests will increase as a result (Lindenmayer and Noss 2006). Although the impact on wildlife species due to post wildfire salvage logging operations has been studied (e.g., Lindenmayer et al. 2004, Hutto and Gallo 2006, Saab et al. 2009, 2011), knowledge is lacking on the influence of post-beetle epidemic harvests (Saab et al. 2014). Focusing on woodpecker population persistence may prove to be an

efficient and comprehensive way for managers to ensure that goals are met related to harvest and maintaining biodiversity. Post-beetle salvage logging practices should consider site-specific snag retention to provide cavity-nesting birds with adequate food and nesting resources (Hutto 2006, Russell et al. 2007, Saab et al. 2009, 2011).

Aspen woodlands (riparian and snow-melt drainages) have been identified as critical habitat for avian diversity, particularly for cavity-nesting birds (Westworth and Telfer 1993, Dobkin et al. 1995, Hobson and Bayne 2000, Aitken and Martin 2004, Newlon and Saab 2011). The importance of aspen groves to nesting woodpeckers after post-disturbance harvest has been demonstrated by large numbers of nest cavities in aspen relative to harvested areas (Kronland and Restani 2011). With the potential of increased salvage logging in beetle-affected pine forests, retention of available aspen groves will likely minimize impacts to avian community structure and diversity (Drever and Martin 2010, Saab et al. 2014, this study).

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APPENDICES

APPENDIX A

PEARSON'S CORRELATION RESULTS FOR *PICOIDES* SPP. COVARIATES

Appendix A: Pearson's correlation results for *Picoides* spp. (American three-toed, hairy, and downy woodpeckers) comparing non-MPB covariates (Nht = height of the nest cavity; DBH = diameter-at-breast height of the nest tree; Aspen = nest tree genus: *Populus* or *Pinus*) MPB covariates (MPB_{per} = pre- [2003-2006] or post-epidemic [2009-2013]; AM_{1ha} & AM_{314ha} = annual tree-mortality at local- and landscape-scales, respectively; CM_{1ha} & CM_{314ha} = cumulative tree-mortality at local- and landscape-scales, respectively), and a RESQ covariate ($RESQ_{max}$ = maximum RESQ count at a nest applied from the closest point-count location).

	DBH	Aspen[a]	MPB_{per}[b]	AM_{1ha}	AM_{314ha}	CM_{1ha}	CM_{314ha}	$RESQ_{max}$
Nht	0.654	-0.076	-0.009	-0.031	0.003	-0.028	-0.015	-0.062
DBH		-0.436	0.161	-0.065	-0.043	0.162	0.170	-0.099
Aspen[a]			-0.349	-0.054	-0.039	-0.413	-0.293	0.104
MPB_{per}[b]				0.251	0.265	0.809	0.958	-0.503
AM_{1ha}					0.941	0.200	0.144	0.017
AM_{314ha}						0.152	0.151	-0.003
CM_{1ha}							0.820	-0.431
CM_{314ha}								-0.493

[a]Reference condition for Aspen is the genus *Pinus*

[b]Reference condition for MPB_{per} is the pre-epidemic period (2003-2006)

APPENDIX B

PEARSON'S CORRELATION RESULTS FOR NORTHERN FLICKER COVARIATES

Appendix B: Pearson's correlation results for northern flicker (NOFL) comparing non-MPB covariates (Nht = height of the nest cavity; DBH = diameter-at-breast height of the nest tree; Aspen = nest tree genus: *Populus* or *Pinus*) MPB covariates (MPB_{per} = pre- [2003-2006] or post-epidemic [2009-2013]; AM_{1ha} & AM_{314ha} = annual tree-mortality at local- and landscape-scales, respectively; CM_{1ha} & CM_{314ha} = cumulative tree-mortality at local- and landscape-scales, respectively), and a RESQ covariate ($RESQ_{max}$ = maximum RESQ count at a nest applied from the closest point-count location).

	DBH	Aspen[a]	MPB_{per}[b]	AM_{1ha}	AM_{314ha}	CM_{1ha}	CM_{314ha}	$RESQ_{max}$
Nht	0.367	-0.305	0.135	-0.318	-0.312	0.032	0.153	-0.127
DBH		-0.854	0.110	-0.305	-0.327	0.075	0.177	-0.099
Aspen[a]			-0.124	0.215	0.220	-0.118	-0.184	0.167
MPB_{per}[b]				0.251	0.263	0.842	0.978	-0.527
AM_{1ha}					0.969	0.227	0.166	0.072
AM_{314ha}						0.201	0.188	0.030
CM_{1ha}							0.830	-0.399
CM_{314ha}								-0.543

[a]Reference condition for Aspen is the genus *Pinus*

[b]Reference condition for MPB_{per} is the pre-epidemic period (2003-2006)

APPENDIX C

PEARSON'S CORRELATION RESULTS FOR RED-NAPED SAPSUCKER COVARIATES

Appendix C: Pearson's correlation results for red-naped sapsucker (RNSA) comparing non-MPB covariates (Nht = height of the nest cavity; DBH = diameter-at-breast height of the nest tree) MPB covariates (MPB_{per} = pre- [2003-2006] or post-epidemic [2009-2013]; AM_{1ha} & AM_{314ha} = annual tree-mortality at local- and landscape-scales, respectively; CM_{1ha} & CM_{314ha} = cumulative tree-mortality at local- and landscape-scales, respectively), and a RESQ covariate ($RESQ_{max}$ = maximum RESQ count at a nest applied from the closest point-count location).

	DBH	MPB_{per}[a]	AM_{1ha}	AM_{314ha}	CM_{1ha}	CM_{314ha}	$RESQ_{max}$
Nht	0.432	0.034	-0.171	-0.047	-0.019	0.045	-0.095
DBH		0.192	-0.050	0.099	0.105	0.187	-0.202
MPB_{per}[a]			0.345	0.422	0.888	0.987	-0.622
AM_{1ha}				0.855	0.370	0.290	-0.132
AM_{314ha}					0.312	0.346	-0.186
CM_{1ha}						0.904	-0.570
CM_{314ha}							-0.617

[a]Reference condition for MPB_{per} is the pre-epidemic period (2003-2006)

APPENDIX D

PEARSON'S COVARIATE CORRELATION RESULTS FOR TIME-VARYING COVARIATES

Appendix D: Pearson's correlation results for 5 species of woodpecker (American three-toed, hairy, and downy woodpeckers, northern flicker, and red-naped sapsucker) comparing time-varying non-MPB covariates (T_{max} = maximum daily temperature, P_{prev} = amount of precipitation fallen on the previous day, Day = day-of-season, Day^2 = day-of-season squared). Values correspond to a standard breeding season (from day 1 on May 17th to day 76 on July 31st) across nine years (2003-2006, 2009-2013).

	P_{prev}[a]	Day	Day^2
T_{max}[a]	-0.257	0.692	0.67
P_{prev}[a]		-0.259	-0.241
Day			0.967

[a] Data from nearest SNOTEL site: #893, Tizer basin, MT (http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=893&state=mt)

APPENDIX E

SUMMARY STATISTICS FOR NON-MPB COVARIATES BY MPB PERIOD

Appendix E: Pearson's correlation coefficients between non-MPB covariates (Nht = height of the nest cavity; DBH = diameter-at-breast height of the nest tree; Aspen = % of nests found in aspen) MPB period (Pre = 2003-2006, Post = 2009-2013) with sample sizes (n.pre, n.post) for nests of *Picoides* spp. (American three-toed, hairy, and downy woodpeckers), northern flicker (NOFL), and red-naped sapsucker (RNSA).

		Pre [mean (SD)]	n.pre	Post [mean (SD)]	n.post
	T_{max}	17.1 (6.8)	368 days	17.3 (6.8)	460 days
	P_{prev}	0.09 (0.23)	364 days	0.10 (0.19)	455 days
Picoides spp.	Nht	9.1 (4.8)	39 nests	9.0 (4.2)	158 nests
Picoides spp.	DBH	28.5 (12.3)	39 nests	33.0 (10.2)	158 nests
Picoides spp.	%Aspen	94.90%	39 nests	52.20%	158 nests
NOFL	Nht	8.0 (2.1)	15 nests	9.1 (4.1)	37 nests
NOFL	DBH	35.4 (13.5)	15 nests	38.6 (13.5)	37 nests
NOFL	%Aspen	80%	15 nests	67.60%	37 nests
RNSA	Nht	9.1 (4)	56 nests	9.2 (3.4)	67 nests
RNSA	DBH	30.0 (6.9)	56 nests	32.9 (7.8)	67 nests
RNSA	%Aspen	100%	56 nests	100%	67 nests

APPENDIX F

RELATIVE DENSITIES OF HATCHED NESTS

Appendix F: Year-specific values of hatched nests found by species in the Elkhorn Mountains of Montana. Species abbreviations refer to American three-toed, hairy, and downy woodpeckers, northern flicker, and red-naped sapsucker; ATTW, HAWO, DOWO, NOFL, and RNSA, respectively. *Picoides* Total is a sum of hatched nests for ATTW, HAWO, and DOWO. Shown in bold: Total pre-MPB = sum of hatched nests 2003-2006; Total post-MPB = sum of hatched nests 2009-2013; Overall total = sum of hatched nests all years. No research was conducted during 2007 or 2008.

Year	ATTW	HAWO	DOWO	*Picoides* Total	NOFL	RNSA
2003	1	4	4	9	5	8
2004	2	7	4	13	3	16
2005	2	5	2	9	3	17
2006	2	3	2	7	2	14
Total pre-MPB	**7**	**19**	**12**	**38**	**13**	**55**
2009	7	7	7	21	1	9
2010	7	9	4	20	3	10
2011	10	9	7	26	8	14
2012	11	13	25	49	10	15
2013	9	17	9	35	13	15
Total post-MPB	**44**	**55**	**52**	**151**	**35**	**63**
Overall total	**51**	**74**	**64**	**189**	**48**	**118**