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Research Article

Woodpecker Nest Survival, Density, and a Pine Beetle Outbreak

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ABSRACT Mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in western North American coniferous forests are increasing in size and severity. An understanding of wildlife population responses to pine beetle outbreaks is needed to inform habitat conservation strategies. We monitored 355 nests of 5 woodpecker species during 2 sampling periods, before (2003–2006) and after (2009–2014) the peak of a pine beetle outbreak in dry mixed conifer forest of Montana, USA. Three of 5 woodpecker species represented the beetle-foraging group: American three-toed (*Picoides dorsalis*), hairy (*Dryobates villosus*), and downy (*D. pubescens*) woodpeckers. The other 2 species studied were northern flicker (*Colaptes auratus*), a foraging and habitat generalist, and red-naped sapsucker (*Sphyrapicus nuchalis*), a sap forager and bark-gleaning insectivore. We analyzed daily survival rate of nests in relation to pine beetle outbreak (445,000 ha) severity and timing, along with covariates unrelated to the outbreak (temp, nest height, and nest tree diameter). Our results provided stronger evidence for relationships between woodpecker nest survival and the non-outbreak variables than those associated with outbreaks. Our results indicated limited support for nest survival relationships with beetle severity (annual and cumulative pine tree mortality at 0.81-ha and 314-ha scales). Nevertheless, we observed a significant increase in densities of hatched nests for beetle-foraging woodpeckers following the outbreak. Our results suggest that woodpeckers, particularly beetle foragers, respond numerically to pine beetle outbreaks through increased nesting densities more so than functionally via nest survival. © 2019 The Authors. *Journal of Wildlife Management* Published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS *Dendroctonus ponderosae*, mountain pine beetle, nest density, nest survival, Picidae, *Pinus ponderosa*, ponderosa pine, woodpeckers.

Large-scale disturbances (e.g., wildfire, bark beetle [Scolytinae] outbreaks) in western North American forests influence forest structure and composition. Land management practices and climate change have altered disturbance regimes of many western North American forests (Attiwill 1994, Parker et al. 2006, Raffa et al. 2008, Bentz et al. 2010). Mountain pine beetle (*Dendroctonus ponderosae*; pine beetle) outbreaks have increased in size and severity over the last century with implications for biological diversity and ecological services (Kurz et al. 2008, Cudmore et al. 2010, Sambaraju et al. 2012). Outbreaks can negatively affect recreational opportunities, economic resources, and habitat for some wildlife while generating economic opportunity (e.g., for salvage logging) and habitat for wildlife dependent on dead trees (e.g., woodpeckers; Safranyik and Wilson 2006, Kaufmann et al. 2008). Forest managers are often challenged with meeting socioeconomic objectives while maintaining habitat for wildlife. A clear understanding of bark beetle effects on wildlife populations is needed to inform management decisions regarding habitat for species of conservation concern (Saab et al. 2014).

The mountain pine beetle is a native bark beetle that colonizes several host tree species (primarily *Pinus* spp.) including lodgepole (*Pinus contorta*) and ponderosa pine (*P. ponderosa*; Sartwell and Stevens 1975). At endemic levels, the pine beetle causes mortality of relatively few susceptible host trees, but during outbreaks, large numbers of beetles overcome the defenses of healthy trees, resulting in widespread and severe pine mortality (Powell et al. 2012, Sambaraju et al. 2012). Past management practices that resulted in even-aged and structurally homogeneous forests increased forest susceptibility to pine beetle outbreaks (Fettig et al. 2007). Additionally, the lack of extended, cold winter temperatures

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(i.e., ≤−35 °C) has decreased winter pine beetle mortality and thereby increased potential for outbreak dynamics (Régnière and Bentz 2007, Bentz et al. 2010, Sambaraju et al. 2012). Furthermore, climate models predict conditions allowing future range expansion of the mountain pine beetle northward and into higher elevations, likely broadening the geographic extent of outbreak conditions (Williams and Liebhold 2000, Bentz et al. 2010, Sambaraju et al. 2012).

Pine beetle outbreaks affect wildlife populations differently depending upon the life history of each species (Saab et al. 2014). Outbreaks benefit many species, such as woodpeckers and other cavity-nesting birds, by generating snags that provide nesting and foraging resources. Many woodpecker species benefit by snag-generating disturbances that result in increased foraging and nesting substrates (Hutto 1995, Saab et al. 2007, Edworthy et al. 2011), and recently disturbed forests may support source populations for additional less-specialized species (Ostfeld and Keesing 2000, Runge et al. 2006). Researchers in British Columbia, Canada reported evidence for increases in nest densities following a pine beetle outbreak but no changes in measured components of fecundity (Edworthy et al. 2011).

Woodpeckers represent focal species for forest management because cavities excavated for nesting are used by a variety of other wildlife species (Martin and Eadie 1999, Martin et al. 2004, Virkkala 2006) and because woodpeckers are responsive to forest management activities (Saab et al. 2007). Management activities designed to reduce pine beetle outbreaks or mitigate negative socioeconomic effects of outbreaks, such as fuels reduction and salvage logging, could adversely influence woodpecker populations (Lindenmayer and Noss 2006, Safranyik and Wilson 2006, Saab et al. 2014, Thorn et al. 2018).

We studied nesting woodpeckers before and during a pine beetle outbreak that peaked in 2008 on the Helena National Forest in Montana, USA. We monitored nests of 5 woodpecker species, representing 3 foraging strategies, for 4 years before and 6 years after the peak of a pine beetle outbreak. Three of the 5 woodpecker species commonly consume bark beetle (Scolytinae) larvae: American three-toed (*Picoides dorsalis*), hairy (*Dryobates villosus*), and downy (*D. pubescens*) woodpeckers. The other 2 species studied were northern flicker (*Colaptes auratus*), a resource generalist, and red-naped sapsucker (*Sphyrapicus nuchalis*), a sap forager and bark-gleaning insectivore.

Beetle-foraging woodpeckers are bark drillers whose food resources include adult and larval stages of bark (*Dendroctonus* spp., *Scolytus* spp.) and wood-boring (Coleoptera) beetles obtained by excavating trees and snags (Jackson and Ouellet 2002, Jackson et al. 2002, Tremblay et al. 2018). Relationships of nest survival with pine beetle outbreaks may vary, however, due to differences in nest initiation dates and preferred nest tree characteristics, factors that influence daily nest survival (Grant et al. 2005, Bonnot et al. 2008, Saab et al. 2011).

The northern flicker is considered a ground-foraging woodpecker because it feeds primarily on ground-dwelling arthropods (mainly adult and larval ants; family Formicidae) but also consumes adult and larval beetles and a variety of fruits and seeds (Wiebe and Moore 2017). Primary foraging substrates (i.e., downed logs) and associated prey items (ants) of flickers can be positively affected by pine beetle outbreaks (Bull et al. 2007). The flicker favors nesting in decay-prone aspen woodlands but will nest in pines with suitable decay (Wiebe 2001, Aitken et al. 2002, Martin et al. 2004, Wiebe and Moore 2017).

The red-naped sapsucker principally nests in live aspen and obtains most of its food by consuming sap and cambium of predominantly deciduous trees during the breeding season (Dobkin et al. 1995, Martin et al. 2004, Walters et al. 2014). Additionally, this species opportunistically feeds on insects that are trapped in sap (especially ants and small flying insects) (Walters et al. 2014). Feeding requirements of the sapsucker place them in association with live trees (often in aspen [*Populus* spp.] woodlands) as compared with beetle-foraging species and flickers.

Nest survival patterns of cavity-nesting birds also vary in relation to weather, nesting date, and nest site characteristics (Wiebe 2001, Paclík et al. 2009, Saab et al. 2011, Kozma and Kroll 2012). Older, more experienced woodpeckers frequently initiate nesting earlier in the season and are more successful than younger birds (Wiktander et al. 2001, Pechacek 2006).

Nests excavated at greater heights and in larger-diameter trees likely have greater protection from predators and inclement weather than lower nest cavities placed in smaller diameter trees (Li and Martin 1991, Wiebe 2001). Warmer temperatures typically increase activity and availability of insect prey (e.g., ants, bark beetles, and butterflies [Lepidoptera]) consumed by woodpeckers (Elchuk and Wiebe 2003, Rossmanith et al. 2007, Gaylord et al. 2008). Thus, temperature could moderate effects of pine beetle outbreaks on nest survival for beetle-foraging species, whereby elevated temperatures could adversely affect nest survival in areas of high conifer mortality with greater solar exposure (Neal et al. 1993, Conway and Martin 2000, Saab et al. 2011).

Our objectives were to examine woodpecker nest survival relationships with the timing and severity of a mountain pine beetle outbreak, examine the relative influence of non-pine beetle factors on nest survival in the context of outbreak-related effects, and compare woodpecker nest densities before versus after the peak of a pine beetle outbreak. We had several predictions about species' responses based on their life histories. We predicted strong positive responses to the pine beetle outbreak via increased daily survival rates (DSR) and densities for the beetle-foraging species and northern flicker. We predicted that DSR and nesting density of the red-naped sapsucker would remain unaffected by a pine beetle outbreak. For all woodpecker species in our study, we expected that nest survival would decline with increasing day in the nesting season, and improve with increasing nest heights, diameter of nest trees, and temperature. We expected pine beetle-related covariates to influence nest survival more than non-pine beetle factors for beetle-foraging woodpeckers, whereas we expected the opposite for northern flickers and red-naped sapsuckers.

STUDY AREA

We conducted this study in the Elkhorn Wildlife Management Unit (121,406 ha) of the Helena National Forest,

Montana (46°46' N, 111°91' W) from 2003–2014. The wildlife management unit is managed primarily for elk (*Cervus canadensis*) by the United States Department of Agriculture (USDA) Forest Service and the Bureau of Land Management. The study area consisted of dry mixed coniferous forest dominated by ponderosa pine with lesser amounts of lodgepole pine and Douglas-fir (*Pseudotsuga menziesii*) in mountainous terrain ranging from 1,500 m to 1,700 m in elevation. The study area was interspersed with snow-melt drainages and riparian areas dominated by quaking aspen (*Populus tremuloides*). April through June were the wettest months in our study area. Average daily temperature and precipitation during May–July were 15 °C and 45 mm, respectively.

We established 4 study units in 2002–2003 ranging 135–270 ha in size and 1,500–1,700 m in elevation. These units were originally intended for studies of prescribed fire effects on bird communities, and represented comparable forest structure, vegetation composition, and topography (Hollenbeck et al. 2013). Prescribed fire treatments were not implemented because of litigation over the proposed treatments. Avian population and community monitoring occurred in 2003–2006, providing pre-outbreak data. A mountain pine beetle outbreak spanning >445,000 ha and including our study units began in 2006 and peaked in 2008 (Crabb and Stoner 2011). We resumed data collection in 2009–2014 to monitor population changes related to outbreak conditions (i.e., 70–80% mortality of pines). Forest conditions in snow-melt drainages and riparian areas remained relatively unchanged throughout the study.

METHODS

Nest Searching and Monitoring

We conducted nest surveys throughout the 4 study units (747 ha) in 2003–2006 and 2009–2014. We conducted 2 surveys each year during the breeding season (15 May–4 Jul) along belt transects, which provided complete coverage of study units. Surveyors broadcast species-specific recordings of calls and drumming to elicit responses by breeding individuals and thereby aid in their detection. Surveyors then used various behavioral and non-behavioral cues to locate nest cavities for individuals whose breeding territories intersected study units (Dudley and Saab 2003).

Once located, surveyors visited nest cavities every 2–5 days to record status and activity until fledging or failure. Surveyors used observations of nest contents and behavior to determine nest status. A portable camera system (Tree Top II System, Sandpiper Technologies, Manteca, CA, USA) allowed surveyors to directly observe the contents of cavities ≤10 m above ground. We also considered observations of adult behavior when determining status of nests inaccessible to the camera system. For example, observations of an adult remaining in the cavity for long periods or adults switching positions indicated incubation, whereas frequent feeding by adults or the sound of begging indicated nestlings (Dudley and Saab 2003, Saab et al. 2007). To determine nest completion (failure or success), surveyors observed nests for ≥2 30-minute periods with no activity. Surveyors often obtained additional evidence for a fate (e.g., ≥1 fledgling near the cavity, destruction of the cavity, broken eggs, dead nestlings). We considered a nest successful if ≥1 young at fledging age left the cavity. We also considered nests successful if we observed an empty cavity with no nestling remains at approximately fledging age. We excluded data from 1 downy woodpecker nest whose fate we were unable to determine. We monitored all nests to completion as described above to inform analysis of nest survival during 2003–2006 and 2009–2013. In 2014 we monitored nests only through hatching to estimate temporal changes in nesting densities (described further below).

Covariates for Analyzing Nest Survival

We compiled 5 spatial and temporal metrics of the pine beetle outbreak and 6 potentially important non-pine beetle factors for use as covariates in nest survival analyses. A categorical covariate distinguished between pre- and post-outbreak years (2003–2006 and 2009–2013, respectively), and 4 covariates derived from remotely sensed data quantified spatial variation in outbreak severity during post-outbreak years. We quantified spatial variation in severity as annual and cumulative pine tree mortality at nest-site (0.81 ha, reported as 1 ha) and home range (314 ha or 1-km radius) scales (i.e., local and landscape scales, respectively). We selected the landscape scale of 314 ha to incorporate the largest home ranges reported for any study species (Walters et al. 2014 [red-naped sapsucker, ranged 1.4 km from nest site], Tremblay et al. 2018 [American three-toed woodpecker, 304 ha]). We derived pine beetle tree mortality metrics from aerial detection survey data, whereby we used model-based methods to translate raw polygon data into 30-m-pixel rasters quantifying annual number of pine trees killed/ha (Crabb and Stoner 2011). We acquired model-based spatial predictions of annual mortality data for years when these predictions were informative (2007–2011). Mortality was negligible during other years (2003–2006, 2012–2013) so we assigned all pixels the average estimated tree mortality for each of these years (0 in 2003–2006, 3 in 2012, and 0 in 2013; Crabb and Stoner 2011). For each year, we derived raster layers quantifying cumulative tree mortality by summing annual mortality layers for all years preceding and including the focal year. We considered annual tree mortality to represent the distribution of active infestation and greatest availability of bark beetle prey. We considered cumulative tree mortality to represent the distribution of standing and fallen dead wood, which provides additional foraging and nesting opportunities for woodpeckers. We used neighborhood analyses to calculate mean annual and cumulative mortality values at local and landscape scales. We conducted all processing of spatial data using ArcGIS software (Environmental Systems Research Institute, Redlands, California, USA).

Non-pine beetle covariates quantified daily weather, day of season, and characteristics of the nest site. We recorded daily maximum temperature and daily precipitation at the nearest Snow Telemetry (SNOTEL) station approximately 14 km southeast of the study area (Snow Telemetry site 893, Tizer Basin, MT). We related DSR to precipitation values from the previous day to represent the potential lagged-effects of

precipitation on food resources and nestlings. We considered linear and quadratic representations of day of season (day 1 corresponded with 17 May) to evaluate seasonal variation in nest survival (Kozma and Kroll 2012). Having drawn values from a weather station rather than at the nest site, daily maximum temperature and daily precipitation strictly represent temporal rather than spatial variation in weather. The nest survival models we used allowed us to analyze nest survival relationships with daily values rather than mean values for observation intervals (Rotella et al. 2004). Finally, we considered nest height, diameter at breast height (1.4 m) of the nest tree (DBH), and nest tree genus (pine = 0, aspen = 1) as covariates of nest survival.

For beetle-foraging species, we included additional covariates to distinguish among species. A categorical species covariate with hairy woodpecker as the reference level allowed differences in mean nest survival estimates. Additionally, we used covariates supported in preliminary analysis of individual species to interact with the species covariate in the final model (described further below).

Statistical Analyses

Nest survival.—We modeled DSR of nests as a function of continuous and categorical covariates using generalized linear models describing daily fate (0 = survived; 1 = failed) as independent Bernoulli trials (Dinsmore et al. 2002, Rotella et al. 2004). Specifically, we modeled DSR as a logit-linear function of covariates:

$$logit\left(\widehat{DSR}_i\right) = \beta_0 + \sum_{j=1}^{J} \beta_j x_{ij},$$

where DSR on day i depends on J covariates (Rotella et al. 2004). We fitted models using Program MARK (White and Burnham 1999) operated from R (R Core Team 2013) via the package RMark (Laake 2013). This approach assumes unambiguous and accurate assignment of nest fates and homogeneity of nest survival rates on any day for a given set of covariate values. Additionally, this approach improves upon historical approaches by calculating likelihoods for intervals based on daily values without requiring assumptions regarding the timing of success or failure within a given interval (Rotella et al. 2004). To facilitate interpretation and comparison with other studies, we translated DSR estimates to nesting period survival (laying + incubation + nestling stages; hereafter overall survival) estimates:

$$\widehat{NSR} = \widehat{DSR}^d,$$

where d is the number of days from nest initiation to fledging (d = 40.5, 39, 46, 45.5, and 44 for American three-toed woodpecker, downy woodpecker, hairy woodpecker, northern flicker, and red-naped sapsucker, respectively; Dudley and Saab 2003). We quantified variance in nesting period survival rate using the delta method (Powell 2007).

For analysis purposes, we grouped the 3 beetle-foraging species but also allowed some differences in nest survival patterns among species by including species as a blocking factor and considering interactions between species and other covariates. This approach pooled limited samples of these species in recognition of their similar life histories, while allowing species-specific variation as supported by available data determined by model selection.

We selected models for inference from candidate models using an information-theoretic approach (Burnham and Anderson 2002). We mainly considered additive covariate effects. We also considered some interactions for beetle-foraging species (i.e., modulation of temperature effects during outbreak conditions [daily maximum temperature × pine beetle period]; Neal et al. 1993, Conway and Martin 2000, Saab et al. 2011) and interactions with species. For each additive model with a pair of covariates of interest for an interaction, we considered an equivalent model with that interaction. To avoid unmanageably large candidate model sets, we screened covariates based on preliminary models fitted to individual beetle-foraging species (American three-toed, hairy, and downy woodpeckers). We only allowed parameters statistically supported for ≥1 individual species to interact with species in models fitted to the complete beetle-foraging species dataset. When evaluating individual-species models, we considered relationships supported if they appeared in models within 2 Akaike's Information Criterion adjusted for small samples (AIC_c) of the top-ranked model ($AIC_c = 0$) and ranked above the intercept-only model, and if the 95% confidence intervals of their parameter estimates excluded zero.

For each species (or group), we constructed and selected models in 2 sequential steps, wherein we used AIC_c to rank models. During step 1, we considered an exhaustive model set representing potential non-pine beetle covariate combinations, from which we retained models within 2 AIC_c units of the top-ranked model that only included informative parameters (i.e., 95% CIs excluded zero; Arnold 2010). During step 2, we ranked models representing all possible ways of combining pine beetle covariates with non-pine beetle covariate combinations represented by models retained in step 1. We retained the top-ranked model in step 2 for inference. In addition, we used the highest-ranked model containing the pine beetle period parameter to further evaluate species-specific predictions in relation to the pine beetle outbreak. To avoid multicollinearity of predictor variables, we excluded highly correlated covariate pairs ($r \geq 0.65$) from individual models (Neter et al. 1996). Day of season and maximum daily temperature were highly correlated (Pearson's $r = 0.69$) and therefore never in the same model. Additionally, nest tree genus was invariant and therefore not considered in red-naped sapsucker models (all nests were in aspen). We included woodpecker species as a covariate in all models for the beetle-foraging group to account for differences in nest survival among the 3 species. Because annual and cumulative tree mortality were set to zero before outbreak, models with any of these covariates always included pine beetle period to differentiate pre- from post-outbreak tree mortalities of zero.

Nest density.—We quantified annual densities of hatched nests only (rather than all nests) to evaluate numerical

Table 1. Number of nests monitored (n), number of failures (F), and number of exposure days for nest survival analysis ($n_{effective}$) by species and pine beetle period (pre-beetle = 2003–2006; post-beetle = 2009–2013; total = both) in western Montana, USA. Data for beetle-foraging species (American three-toed woodpecker, hairy woodpecker, and downy woodpecker) were combined for analysis with species as a covariate.

	Pre-pine beetle			Post-pine beetle			Total		
Species	n	F	$n_{effective}$	n	F	$n_{effective}$	n	F	$n_{effective}$
Beetle-foraging species	39	11	748	157	24	2,731	196	35	3,479
American three-toed woodpecker	8	4		45	6		53	10	
Hairy woodpecker	19	6		58	14		77	20	
Downy woodpecker	12	1		54	4		66	5	
Northern flicker	15	5	328	37	6	938	52	11	1,266
Red-naped sapsucker	57	11	1,616	67	10	1,950	124	21	3,566

responses to the pine beetle outbreak because we lacked data to formally estimate nest detectability. Based on high nest detection rates (>90% of woodpecker nests) during the nestling period (Russell et al. 2009), we assumed detectability to be sufficiently high for hatched nest densities to accurately represent temporal change. We compiled the number of hatched nests observed per 40 ha for each study unit in each year (i.e., hatched nest densities). We plotted mean and 95th percentiles for density in each year ($n = 4$ study units) to assess numerical changes. We used an order statistic approximately unbiased for normally distributed data to estimate 95th percentiles for density (i.e., quantile function in R with type = 9).

RESULTS

We monitored 53, 77, and 66 nests of American three-toed, hairy, and downy woodpeckers, respectively, or 196 nests for the beetle-foraging species from 2003–2006 and 2009–2013 (Table 1). We also monitored 52 northern flicker and 124 red-naped sapsucker nests during the 9-year study period. Covariate values between pre- and post-pine beetle outbreak varied sufficiently among nests to warrant their inclusion in nest survival models (Tables A1 and A2). Highly correlated variables ($r \geq 0.65$) were never considered together in the same models (Tables S1–S4, available online in Supporting Information).

For beetle-foraging species, we only found statistical support for DSR relationships with non-pine beetle covariates (Table 2, Table B1). Based on preliminary models fitted to individual species (Table B2), we allowed maximum daily temperature, tree diameter (DBH), and pine beetle period to interact with species. The best-supported nest survival model for beetle-foraging species described an interactive effect of maximum daily temperature with species, along with an overall (linear) effect of nest tree diameter (DBH). Adding pine beetle covariates to this model reduced model rank (Table 2), and confidence intervals overlapped zero for additional covariate relationships appearing in lower-ranked models. The top-ranked model was supported over a model with only the species covariate ($\Delta AIC_c = 6.3$) or no covariates ($\Delta AIC_c = 9.8$). Nest survival related positively with nest tree diameter and positively with daily temperature for hairy and downy woodpeckers, whereas the opposite was true for American three-toed woodpecker in relation to temperature (Table 3; Fig. 1).

Table 2. Model selection from pine beetle candidate models (step 2) for woodpecker nest survival in western Montana, USA, 2003–2013. K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, and ΔAIC_c = model AIC_c − minimum AIC_c (top-ranked model). Covariate descriptions: SPP = species; Tmax = maximum daily temperature (°C); DBH = diameter at breast height; pine beetleper = pine beetle period (0 = 2003–2006, 1 = 2009–2013); AM_{1ha}, AM_{314ha} = annual number of pine trees killed per ha within 0.81 ha (1 ha for notation purposes) and 314 ha of the nest; CM_{1ha}, CM_{314ha} = cumulative number of pine trees killed per ha within 1 ha and 314 ha of the nest. Candidate model sets consisted of 57, 20, and 20 models for beetle-foraging species, northern flicker, and red-naped sapsucker, respectively. Only models presented within 2 AIC_c units of the top-ranked model and the constant daily survival rate models (intercept only) are shown.

Species	**Model**	K	AIC_c	ΔAIC_c
Beetle-foraging species	$SPP + T_{max} + SPP \times T_{max} + DBH$	7	303.4	0.0
	$SPP + T_{max} + SPP \times T_{max} + DBH + CM_{1ha} + \text{pine beetle}_{per}$	9	303.7	0.4
	$SPP + T_{max} + SPP \times T_{max} + DBH + \text{pine beetle}_{per}$	8	305.2	1.8
	$SPP + DBH$	4	305.2	1.9
	SPP	3	309.6	6.3
	Constant	1	313.2	9.8
Northern flicker	Constant	1	99.8	0.0
	Pine beetle_{per}	2	100.0	0.1
	CM_{314ha}	2	100.3	0.4
	AM_{314ha}	2	101.1	1.2
	CM_{1ha}	2	101.4	1.6
	$\text{Pine beetle}_{per} + AM_{314ha}$	3	101.7	1.9
	AM_{1ha}	2	101.8	1.9
Red-naped sapsucker	$Nht + DBH + CM_{1ha}$	4	199.7	0.0
	$Nht + DBH + CM_{1ha} + AM_{1ha}$	5	201.6	1.8
	$Nht + DBH + CM_{1ha} + AM_{314ha}$	5	201.7	2.0
	Constant	1	212.3	12.6

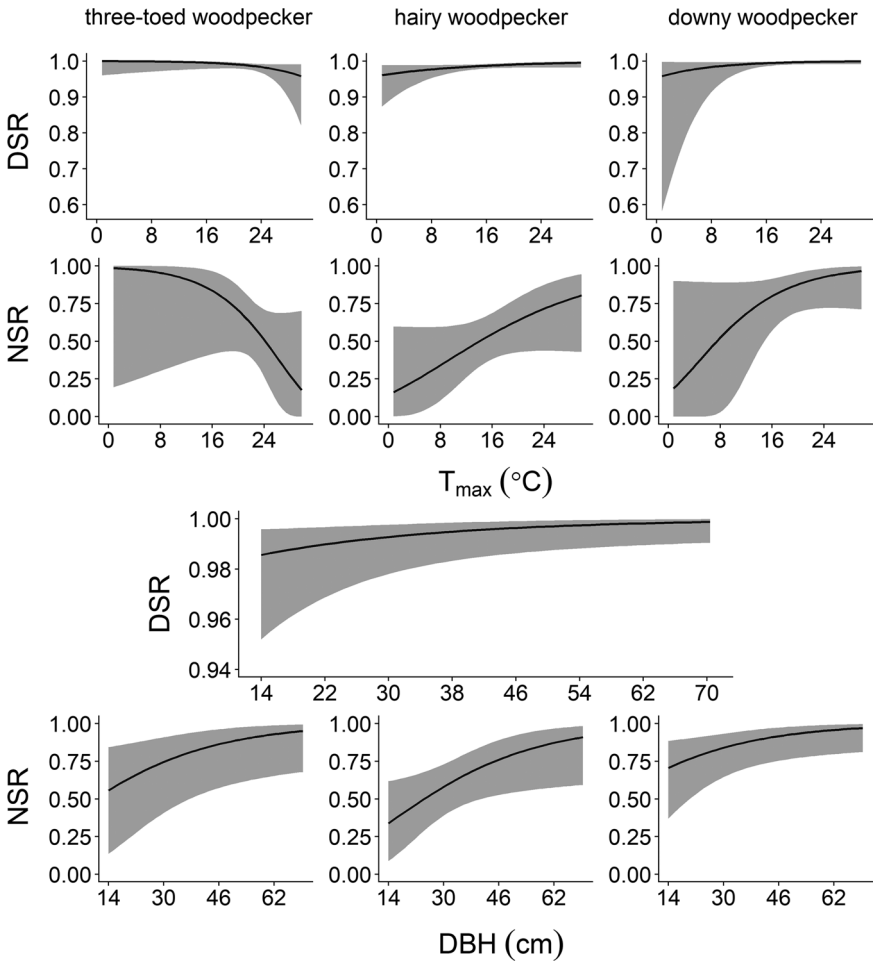

Figure 1. Predicted daily nest survival rates (DSR) and overall nest survival rates (NSR) in relation to statistically supported covariates (max. daily temp [Tmax] in °C, nest tree diameter [DBH] in cm) from the top-ranked model for beetle-foraging woodpeckers in western Montana, USA, 2003–2013. Estimates (solid lines) and 95% confidence bands (shaded) are shown across the range of observed values for a given covariate (*x*-axis) with other covariates fixed at mean values. Daily survival rates related to DBH are the same for all species, but nest survival rates by species reflect differences in nesting period lengths.

We found no evidence for any covariate relationships with nest survival of northern flickers. A model describing nest survival as constant (intercept parameter only) was ranked highest by AIC_c (Table 2, Table B1), and all covariate relationships in lower ranked models overlapped zero. The top-ranked (intercept-only) model estimated a DSR of 0.991 (95% CLs = 0.985, 0.995), resulting in an overall survival of 0.676 (95% CLs = 0.519, 0.832).

We found strong evidence for DSR relationships with 2 non-pine beetle (nest height, DBH) and 1 pine beetle covariate (cumulative tree mortality in 0.81 ha; for notation purposes 1 ha) for red-naped sapsucker (Table 2, Table B1). The top-ranked model was supported over a model with no covariates ($\Delta AIC_c = 12.6$), and confidence intervals included zero for covariate relationships appearing only in lower ranked models. Daily nest survival increased with increasing nest

Table 3. Parameter estimates and 95% confidence limits (LCL, UCL) from the top-ranked nest survival models for woodpeckers in western Montana, USA, 2003–2013. Parameter descriptions: SPP = species; T_{max} = maximum daily temperature (°C); DBH = diameter at breast height (cm); Nht = nest height (m); and CM_{1ha} = cumulative number of pine trees killed per ha within 0.81 ha of the nest. Models were selected from those representing non-pine beetle and pine beetle covariate combinations (step 2). Estimates are for covariates on their original scale (i.e., not transformed or scaled).

Parameter	Beetle-foraging species	Northern flicker	Red-naped sapsucker
Intercept	1.77 (0.13, 3.42)	4.75 (4.16, 5.34)	6.94 (5.11, 8.77)
SPP: three-toed woodpecker	4.91 (−0.16, 9.98)		
SPP: downy woodpecker	−0.13 (−3.31, 3.04)		
T_{max}	0.07 (−0.01, 0.16)		
SPP × T_{max}: three-toed woodpecker	−0.24 (−0.47, −0.01)		
SPP × T_{max}: downy woodpecker	0.06 (−0.12, 0.24)		
DBH	0.04 (0.00, 0.08)		−0.13 (−0.20, −0.06)
Nht			0.26 (0.09, 0.42)
CM_{1ha}			0.01 (0.00, 0.03)

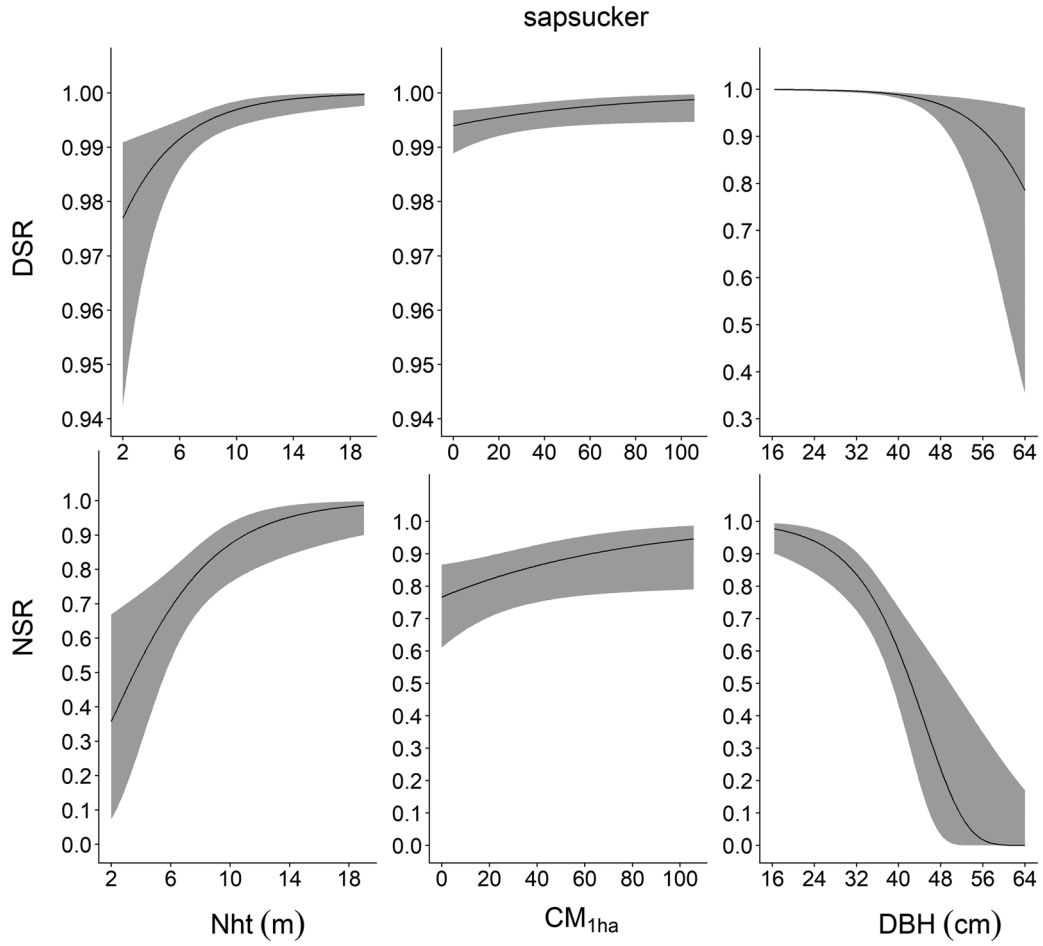

Figure 2. Predicted daily nest survival rate (DSR) and overall nest survival rate (NSR) in relation to statistically supported covariates (nest height [Nht] in m, cumulative tree mortality within 0.81 ha [CM_{1ha}], and nest tree diameter [DBH] in cm) from the top-ranked model for the red-naped sapsucker in western Montana, USA, 2003–2013. Estimates (solid lines) and 95% confidence bands (shaded) are shown across the range of observed values for a given covariate (*x*-axis) with other covariates fixed at mean values.

height and local-scale cumulative tree mortality, and survival decreased with increasing DBH (Table 3, Fig. 2). The nest survival relationship with cumulative tree mortality was notably weaker than relationships with nest height and DBH (Fig. 2).

A pattern of higher nest survival rates was apparent during the post-outbreak compared with the pre-outbreak period for 4 of 5 woodpecker species, but we could not detect a statistical difference (Fig. 3). As expected, mean survival estimates for the red-naped sapsucker differed little between time periods. A positive relationship with pine beetle period was supported for American three-toed woodpecker when analyzed alone (Table B2) despite limited pre-outbreak data (Table 1), a result consistent with our predictions.

Among woodpeckers, only beetle foragers exhibited a definitive increase in nesting densities during post-outbreak years (2009–2014; Fig. 4). Their densities peaked in 2012 and were most distinct from pre-outbreak densities. The confidence interval for 2012 completely excluded those for all pre-outbreak year densities, and the confidence interval for 2013 density substantially overlapped the 2006 interval. Northern flicker hatched nest densities also increased somewhat after the outbreak but were not statistically distinct from pre-outbreak densities. Hatched nests of red-naped sapsuckers varied little between pre- versus post-outbreak periods.

DISCUSSION

Variables unrelated to the outbreak provided more support for explaining nest survival than the outbreak timing or severity across all species groups. This result was consistent with our prediction for northern flicker and red-naped sapsucker but contradicted our expectation for beetle-foraging woodpeckers. Although we estimated higher nest survival rates during the post-outbreak period for 4 of 5 woodpecker species, this difference was not statistically clear. We found a statistically supported increase in nest survival for American three-toed woodpecker when analyzed alone (Table B2). Nevertheless, we found stronger relationships with temperature and tree diameter for beetle-foraging species. The most definitively supported pine beetle relationship with nest survival was for red-naped sapsucker with local-scale cumulative mortality of pine trees. Even this relationship, however, was weaker than relationships with nest height and nest tree diameter.

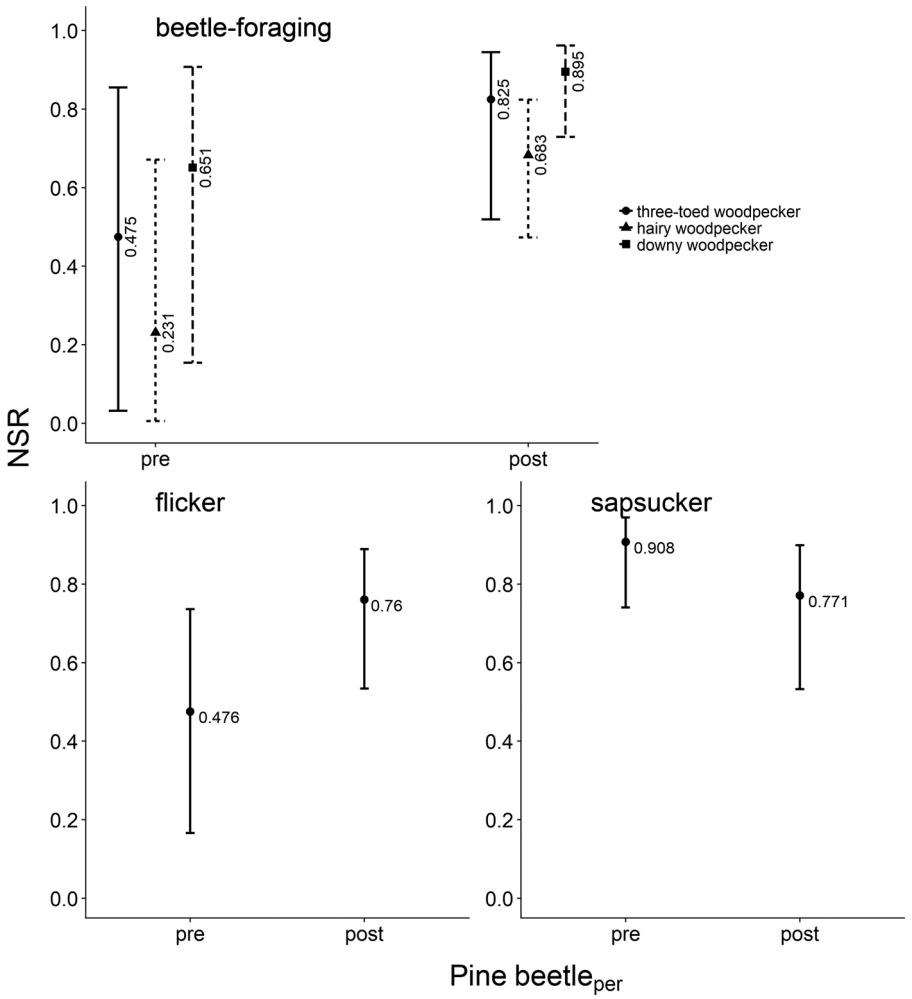

Figure 3. Predicted overall nest survival rates (NSR) pre- versus post-pine beetle outbreak (2003–2006 vs. 2009–2013) for beetle-foraging woodpeckers (American three-toed woodpecker, hairy woodpecker, and downy woodpecker), northern flickers, and red-naped sapsuckers in western Montana, USA, 2003–2013. Estimates (dots) and 95% confidence bands (error bars) are from the top-ranked model for each species group containing the pine beetle$_{per}$ parameter, a categorical covariate distinguishing between pre- and post-pine beetle outbreak. Parameters other than pine beetle$_{per}$ were fixed at their mean values. For beetle-foraging species, daily survival estimates were the same but NSR differed among species because of differences in nesting period lengths.

The notable influence of temperature on nest survival in relation to other factors, including outbreak-related habitat changes, is a documented pattern for woodpeckers (Hollenbeck et al. 2011, Newlon and Saab 2011, Saab et al. 2011). Woodpecker nest survival can relate positively or negatively with temperature, depending on forest characteristics (Towler et al. 2012). The positive relationship between temperature and nest survival for hairy and downy woodpeckers contrasted with the negative relationship for American three-toed woodpeckers; this may be explained by their differential use of nest trees. Hairy and downy woodpeckers nested predominantly in aspen trees, whereas three-toed woodpeckers nested primarily in beetle-killed conifers (Table A1). Additionally, nest survival for all 3 species was higher in larger diameter trees. Large, living trees provide relatively stable and moderate temperatures, whereas nest cavities in smaller, dead trees experience more extreme temperatures (Wiebe 2001). Reduced forest cover in beetle-killed forests could lead to increased ambient temperatures, potentially affecting nest survival of cavity-nesting birds (Neal et al. 1993, Wachob 1996, Conway and Martin 2000). The influence of ambient temperature on incubation behavior and subsequent reproductive effort likely differs in cold versus hot environments (Conway and Martin 2000). Increasing ambient temperatures potentially cause heat stress to eggs and young, particularly in snags of beetle-killed forests with sparse shade.

Annual changes in hatched nest densities were consistent with our predictions for woodpecker population responses to the pine beetle outbreak. Increased nest densities during outbreak years were most pronounced for beetle foragers. Northern flicker nest densities also increased but not as markedly as beetle foragers, whereas red-naped sapsucker nest densities remained constant. These patterns contribute evidence for responsiveness of beetle-foraging woodpeckers to pine beetle and other bark beetle outbreaks. Pine beetle outbreaks may primarily elicit numerical responses, however, rather than functional responses by affecting nest survival.

The numerical response likely tracked a pulse in foraging and nesting substrates made available by the pine beetle outbreak. Dispersing woodpeckers are probably attracted to elevated bark and wood-boring beetle prey populations and the softer wood for cavity excavation offered by snags

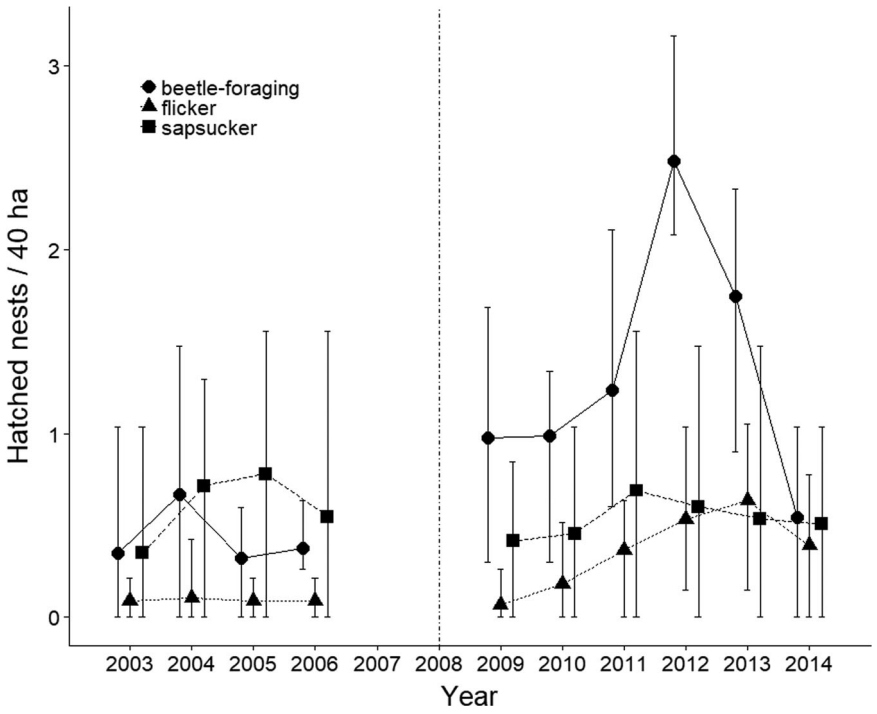

Figure 4. Apparent densities of hatched woodpecker nests (number/40 ha) in the Elkhorn Mountains, Montana, USA, 2003–2014. Beetle-foraging species were American three-toed, hairy, and downy woodpeckers; flicker = northern flicker; and sapsucker = red-naped sapsucker. The dashed vertical line indicates the peak of beetle-induced tree mortality. Means and 95th percentiles are shown in each year ($n = 4$ study units).

(Jackson and Ouellet 2002, Jackson et al. 2002, Tremblay et al. 2018). Higher recruitment or decreased emigration by juveniles out of beetle-infested forests could further influence observed numerical responses (Weatherhead and Forbes 1994, Runge et al. 2006).

Our finding of stronger numerical (nest density) than functional (nest survival) population responses are consistent with other studies. Researchers in British Columbia failed to detect differences in mean fecundity measures (i.e., clutch size and number of nestlings fledged) for the same 3 beetle-foraging species in relation to a pine beetle outbreak (Edworthy et al. 2011). Nest survival is generally high for cavity-nesting birds, potentially restricting responsiveness of this parameter to resource pulses, although published studies tend to report higher nest survival for beetle-foraging woodpeckers in recently fire-disturbed forests (Saab et al. 2005, 2007; Wightman et al. 2010). In addition to providing foraging and nesting opportunities, recently disturbed forests may benefit other components of fitness, such as juvenile or adult survival (Saab and Vierling 2001).

We found little evidence for population responses to the pine beetle outbreak by northern flickers, although their nesting densities tended to increase with time since the peak of beetle outbreak. The number of snags and logs increase after a beetle outbreak. Flickers likely benefit from these resources because they contain favored prey (i.e., ants; Wiebe and Moore 2017).

The lack of patterns in nest survival observed for flickers is consistent with limited evidence in other studies (Wiebe 2001; Saab et al. 2009, 2011; Edworthy et al. 2011) and with characterizations of this species as a resource generalist (Wiebe and Moore 2017). Although Wiebe (2001) reported diameter of the nest tree at cavity height and nest cavity orientation affected temperature of northern flicker nest cavities, she did not find any direct relationships to their hatching or fledging success.

Nesting patterns in relation to the pine beetle outbreak for red-naped sapsuckers were generally consistent with our predictions. As expected, red-naped sapsucker nest survival varied primarily with non-pine beetle factors and densities of hatched nests remained constant following the pine beetle outbreak. Unexpectedly, red-naped sapsucker nest survival was positively related with local-scale cumulative pine tree mortality even though nests were located exclusively in aspen. Local nest predator communities or foraging behavior may differ sufficiently in isolated aspen sites surrounded by beetle-killed conifers to register a difference in nest survival. Such differences were strongly outweighed, however, by apparent effects of nest height and nest tree diameter and were not strong enough to meaningfully affect nest densities.

The negative relationship between red-naped sapsucker nest survival and nest tree diameter was also unexpected. Trade-offs between constraints associated with cavity excavation and nest predation may help explain this unexpected pattern. The red-naped sapsucker is a weak-excavator species that favors nest sites in heartwood rot (*Phellinus tremulae*)-infected aspen, which facilitates cavity excavation (Losin et al. 2006). Heartwood rot is more prevalent in larger, older aspen trees (Basham 1958). Such trees encourage cavity excavation by red-naped sapsuckers, and predators may focus their search images for nests in these larger trees (Tozer et al. 2009). Additionally, black bears (*Ursus americanus*) are frequent predators of sapsucker

nests (Franzreb and Higgins 1975, Hannon and Cotterill 1998, Walters and Miller 2001, Tozer et al. 2009), and larger decayed trees may be easier for bears to climb and access nest cavities. The positive relationship of sapsucker nest survival with nest height is consistent with our prediction of better protection from ground-based nest predators (e.g., black bears likely find higher nests less accessible; Best and Stauffer 1980, Nilsson 1984, Li and Martin 1991, Fisher and Wiebe 2006, Saab et al. 2011).

Sampling of the same study units before and after the peak of a pine beetle outbreak strengthened our inferences regarding population responses. Relatively small sample sizes for beetle-foraging woodpecker nests during the pre-outbreak period, however, limited statistical power for identifying relationships with the outbreak. To improve power, we analyzed data for these 3 species together even though members of this group differed somewhat in their foraging strategies. For example, American three-toed woodpeckers specialize more on resources found in bark-beetle infested forests than other bark-drilling species (Koplin 1969, Murphy and Lehnhausen 1998), and a post-peak outbreak increase in nest survival was statistically supported for this species when analyzed alone (Table B2). Relatively low densities and consequently limited sample sizes likely typify American three-toed woodpecker populations in pine beetle-infested forests, potentially obscuring outbreak-related patterns (Edworthy et al. 2011). Studies in spruce (*Picea* spp.) forests affected by spruce beetle (*Dendroctonus rufipennis*) outbreaks, where this species is more common, could valuably complement our results (Kelly et al. 2018).

The 5-year post-peak outbreak sampling duration may also have limited our inferences. Habitat conditions change substantially 6 years after the peak in tree mortality with increases in deadfall and understory shrub growth (Stone 1995, Page and Jenkins 2007). A longer study may have revealed additional population responses associated with post-disturbance recovery.

MANAGEMENT IMPLICATIONS

Salvage logging has often been applied as a management strategy for economic recovery of timber and to reduce fire risk after forest disturbances of beetle outbreaks and wildfires. Removal of dead and dying trees by salvage logging can result in negative ecological consequences for woodpeckers that rely on snags. Our research highlights the value of beetle-affected forests for several woodpecker species, adding to a larger body of knowledge. In our study, nest survival changed minimally, whereas nest densities increased significantly after the peak of the beetle outbreak. This result suggests that nest densities alone and related site-specific habitat characteristics can be useful to inform post-disturbance management strategies. Additionally, our results suggest that aspen may be an important resource for several woodpecker species (e.g., downy and hairy woodpeckers) to mitigate effects of temperature on nest survival. Mitigating negative effects of temperature and management activities will become increasingly important as beetle outbreaks are expected to become more frequent and severe with a changing climate.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX A. DESCRIPTIVE STATISTICS FOR COVARIATES

Table A1. Descriptive statistics for covariates used to model woodpecker nest survival for beetle-foraging species (American three-toed, hairy, and downy woodpeckers). For day first and last observed, day 1 = 17 May and day 76 = 31 July. Percentage of nests in aspen and monitored post-outbreak are reported for categorical covariates aspen and pine $beetle_{per}$.

		American three-toed woodpecker			Hairy woodpecker			Downy woodpecker		
Covariate type	**Covariate**	$\bar{x}$	**SD**	**Range**	$\bar{x}$	**SD**	**Range**	$\bar{x}$	**SD**	**Range**
Non-pine beetle	Day first observed	36	12.7	12–60	23.7	12.4	1–51	39.3	14.1	13–66
	Day last observed	51.6	8.7	26–69	42.1	12.4	8–71	57.5	10	22–75
	Nht[a]	6.5	2.8	2.3–14.8	10.7	4.7	2.2–25.3	9.1	3.9	2.9–23
	DBH[b]	30.8	8.4	14–51.9	33.6	11.6	17.5–70.4	31	10.8	15.5–70
	Aspen[c]	19%			69%			85%		
Pine beetle	$Pine\ beetle_{per}$[d]	85%			75%			82%		
	AM_{1ha}[e]	4.7	8	0–34.4	3.2	6.6	0–29.1	3.3	7.5	0–33.9
	AM_{1km}[e]	4	6.3	0–22.7	3.1	6	0–22.1	3	6.4	0–22.4
	CM_{1ha}[f]	56.1	30.6	0–106.1	44.9	30.6	0–100.4	50.7	30.7	0–106.1
	CM_{1km}[f]	47.6	21.8	0–70.1	44.1	26.3	0–71.6	48.7	23.8	0–70.6

[a] Height of the nest above ground (m).
[b] Diameter of nest tree (cm) at 1.4 m above ground.
[c] Nest tree genus (0 = *Pinus* spp.; 1 = *Populus* spp.).
[d] Pine beetle period (0 = 2003–2006, 1 = 2009–2013).
[e] Annual number of pine trees killed per ha within 0.81 ha (1 ha) and 314 ha (1 km) of the nest.
[f] Cumulative number of pine trees killed per ha within 0.81 ha (1 ha) and 314 ha (1 km) of the nest.

Table A2. Descriptive statistics for covariates used to model woodpecker nest survival. Beetle-foraging species are American three-toed, hairy, and downy woodpeckers. For day first and last observed, day 1 = 17 May and day 76 = 31 July. Values for maximum daily temperature (T_{max} [°C]) and total precipitation through previous day (P_{prev} [mm]) were summarized across all days any nest was monitored and therefore are the same for all species. Values for nest height (Nht [m]) and diameter at breast height (DBH [cm]) are summarized. Percentage of nests in aspen and monitored post-outbreak are reported for categorical covariates aspen and pine $beetle_{per}$, and percentage of beetle-foraging species nests in each level of species.

		Beetle-foraging species			Northern flicker			Red-naped sapsucker		
Type	**Covariate**	$\bar{x}$	**SD**	**Range**	$\bar{x}$	**SD**	**Range**	$\bar{x}$	**SD**	**Range**
Non-pine beetle	Day first observed	32	15	1–66	22	12	3–52	28	12	4–57
	Day last observed	50	13	8–75	46	13	8–74	57	10	22–75
	T_{max}	18.5	6.4	0.8–29.8	18.5	6.4	0.8–29.8	18.5	6.4	0.8–29.8
	P_{prev}	0.25	0.5	0–55.3	0.25	0.5	0–55.3	0.25	0.5	0–55.3
	Nht	9	4.3	2.2-25.3	8.8	3.6	1.6–19.1	9.1	3.7	2–19
	DBH	32	11	14–70.4	37.7	14	17.4–67.5	31.6	7.5	16.4–64
	Aspen[a]		61%			71%			100%	
Pine beetle	$Beetle_{per}$[b]		80%			71%			54%	
	AM_{1ha}[c]	3.7	7.3	0–34.4	1.3	3.4	0–18.2	2.4	6.4	0–42.8
	AM_{1km}[c]	3.3	6.2	0–22.7	1.2	2.8	0–16.1	2.4	5.4	0–22.1
	CM_{1ha}[d]	49.9	31	0–106	39.4	30	0–89.9	30.1	31	0–106
	CM_{1km}[d]	46.6	24	0–71.6	41.5	27	0–70.3	31.8	30	0–67.1
Species	Spp[e]	HAWO (reference) = 39%; ATTW = 27%; DOWO = 34%			not applicable			not applicable		

[a] Nest tree genus (0 = *Pinus* spp.; 1 = *Populus* spp.).
[b] Pine beetle period (0 = 2003–2006, 1 = 2009–2013).
[c] Annual number of pine trees killed per ha within 0.81 ha (1 ha) and 314 ha (1 km) of the nest.
[d] Cumulative number of pine trees killed per ha within 0.81 ha (1 ha) and 314 ha (1 km) of the nest.
[e] Categorical covariate with 3 levels distinguishing nesting species (HAWO = hairy woodpecker, ATTW = American three-toed woodpecker, and DOWO = downy woodpecker).

APPENDIX B. ADDITIONAL MODEL SELECTION RESULTS

Table B1. Model selection from non-pine beetle candidate models (step 1) for woodpecker nest survival. K = number of parameters, AIC_c = Akaike's Information Criterion corrected for small sample size, and ΔAIC_c = model AIC_c – min AIC_c (top-ranked model). Candidate model sets consisted of 120, 30, and 30 models for beetle-foraging species (American three-toed, hairy, and downy woodpeckers), northern flicker, and red-naped sapsucker, respectively. We included the constant daily survival rate model (intercept only) and models within 2 AIC_c units of the top-ranked model with informative parameters (whose 95% CIs excluded zero). For beetle-foraging species, a model with only the species covariate is also shown for comparison.

Species	**Model**[a]	K	AIC_c	ΔAIC_c
Beetle-foraging species	$Spp + T_{max} + Spp \times T_{max} + DBH$	7	303.4	0.0
	$Spp + T_{max} + Spp \times T_{max} + Nht + DBH$	8	304.5	1.1
	$Spp + T_{max} + Spp \times T_{max} + P_{prev} + DBH$	8	304.8	1.4
	$Spp + DBH$	4	305.2	1.9
	$Spp + T_{max} + Spp \times T_{max} + DBH + Aspen$	8	305.2	1.9
	Spp	3	309.6	6.3
	Constant	1	313.2	9.8
Northern flicker	Constant	1	99.8	0.0
Red-naped sapsucker	$Nht + DBH$	3	201.9	0.0
	Constant	1	212.3	10.4

[a] Spp = categorical covariate with three levels distinguishing nesting species, T_{max} = max daily temperature (°C), DBH = diameter of nest tree (cm) at 1.4 m above ground, P_{prev} = total precipitation through previous day (mm), Aspen = nest tree genus (0 = *Pinus* spp.; 1 = *Populus* spp.), and Nht = height of the nest above ground (m).

Table B2. Nest survival model selection results for individual beetle-foraging species (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 − min AIC_c (top-ranked model). For American three-toed, hairy, and downy woodpeckers, candidate model sets consisted of 39, 30, and 30 models, respectively. Only models presented within 2 AIC_c units of the top-ranked model and equal or better ranked than the constant daily survival rate models (intercept only) are shown for each species. Parameters describing covariate relationships appearing in each model are listed, along with the sign (+ or −) and statistical support (asterisks indicate parameters for which 95% CIs excluded zero) in parentheses.

Species	Model[a]	K	AIC_c	ΔAIC_c
American three-toed woodpecker	$T_{max}(-^*) + AM_{1ha}(-) + CM_{1ha}(-) + \text{Pine beetle}_{per}(+^*)$	5	85.2	0.0
	$T_{max}(-^*) + AM_{1km}(-) + CM_{1ha}(-) + \text{Pine beetle}_{per}(+^*)$	5	85.6	0.4
	$T_{max}(-^*) + CM_{1ha}(-) + \text{Pine beetle}_{per}(+)$	4	85.8	0.6
	$T_{max}(-^*) + AM_{1ha}(-) + \text{Pine beetle}_{per}(+^*)$	4	86.1	0.9
	$T_{max}(-) + DBH(+) + AM_{1ha}(-) + \text{Pine beetle}_{per}(+)$	5	86.3	1.1
	$T_{max}(-) + DBH(+) + AM_{1ha}(-) + CM_{1ha}(-) + \text{Pine beetle}_{per}(+^*)$	6	86.5	1.3
	Constant	1	88.4	3.2
Hairy woodpecker	$T_{max}(+)$	2	167.7	0.0
	DBH(+)	2	169.1	1.4
	Constant	1	169.3	1.6
Downy woodpecker	DBH(+)	2	50.1	0.0
	$T_{max}(+)$	2	51.6	1.6
	$T_{max}(+) + \text{Pine beetle}_{per}(+)$	3	51.9	1.9
	Constant	1	52.0	1.9

[a] T_{max} = max daily temperature (°C), AM_{1ha} = annual number of pine trees killed per ha within 0.81 ha (1 ha) of the nest, CM_{1ha} = cumulative number of pine trees killed per ha within 0.81 ha (1 ha) of the nest, Pine beetle_{per} = pine beetle period (0 = 2003–2006, 1 = 2009–2013), and DBH = diameter of nest tree (cm) at 1.4 m above ground.