

# Mountain Pine Beetle Presence Affects Nest Patch Choice of Red-Breasted Nuthatches

ANDREA R. NORRIS,<sup>1</sup> Forest Sciences Department, University of British Columbia, 3rd Floor Forest Sciences Centre, 3004-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

KATHY MARTIN, Forest Sciences Department, University of British Columbia, 3rd Floor Forest Sciences Centre, 3004-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada, and Environment Canada, Pacific Wildlife Research Centre, 5421 Robertson Road, RR1, Delta, BC V4K 3N28, Canada

**ABSTRACT** The mountain pine beetle (*Dendroctonus ponderosae*) outbreak in western Canada poses significant conservation concern; thus, insights into its effects on wildlife habitat are essential. We used generalized linear mixed models to examine the influence of quaking aspen (*Populus tremuloides*) and mountain pine beetle-infected lodgepole pine (*Pinus contortus*) on nest patch selection of red-breasted nuthatches (*Sitta canadensis*) in central British Columbia, Canada. Prior to the outbreak, nuthatches selected nest patches with 64% more suitable nest trees (standing dead aspen,  $\geq 12.5$  cm dbh) than available (103 trees/ha vs. 63 trees/ha, respectively), but in outbreak years nuthatches chose nest patches with 37% more beetle-infected pine trees than available (63 trees/ha vs. 46 trees/ha, respectively). Our results suggest that nuthatches select sites that maximize nesting and foraging opportunities and, during food pulses, may trade off higher densities of suitable nest trees for higher densities of foraging trees. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):733–737; 2008)

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Red-breasted nuthatches (*Sitta canadensis*) are small-bodied cavity-nesting birds common in old forest stands in western North America (Ghalambor and Martin 1999). In central British Columbia, Canada, nuthatches are year-round residents and typically occupy mature mixed stands of coniferous–deciduous forest, especially where spruce (*Abies* spp.), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) are present (Martin and Norris 2007). During the breeding season, nuthatches are primarily bark- and foliage-gleaning insectivores but will take advantage of the most abundant food supply available, including seeds and berries (Ghalambor and Martin 1999). Nuthatches are classified as facultative weak primary cavity-nesters and will either excavate new nest cavities in dead or decaying trees or use existing cavities.

Nest patch selection by red-breasted nuthatches can be influenced by nest tree condition and availability (Li and Martin 1991, Steeger and Hitchcock 1998, Bunnell et al. 2002, Martin et al. 2004). Decaying hardwood trees are often selected over healthy or coniferous trees because they offer a soft substrate for excavation yet retain a firm shell of sapwood, for stable and secure cavities (Ghalambor and Martin 1999). Red-breasted nuthatches in central British Columbia selected 90% of nests in decaying or dead aspen trees even though these constituted only 10–15% of trees available (Martin et al. 2004). Decaying or dead aspen trees occur at a low frequency in old forests and are further reduced in managed forests (Steeger and Hitchcock 1998).

Food abundance and proximity to foraging habitat can also influence nest patch selection (Li and Martin 1991, Stauss et al. 2005). Nests close to abundant food resources allow adults to make more frequent foraging trips, minimizing time away from the nest and increasing the number of

successful fledglings (Eeva et al. 1989, Stauss et al. 2005). Dead and decaying trees offer greater food availability because they tend to harbor a greater abundance of insects than do healthy trees (Allen et al. 1996). In southeastern British Columbia, the best predictors of nuthatch density were densities of standing dead trees, particularly those killed by mountain pine beetle (*Dendroctonus ponderosae*; Steeger and Hitchcock 1998). In northern Utah, USA, red-breasted nuthatch abundance increased with degree of mountain pine beetle infection in stands of lodgepole pine, up to a maximum of 2 nuthatches/ha in stands with 70% tree mortality (Stone 1995). Although multiple studies found significant associations of nuthatches with diseased trees, our study is the first to document nest and foraging substrate availability and use before and during a major mountain pine beetle outbreak and examine how selection of these 2 resources change with the outbreak (Stone 1995, Steeger and Hitchcock 1998).

Within the last decade, the condition of mixed forests of interior British Columbia has changed drastically due to a mountain pine beetle outbreak (Martin et al. 2006). Our objective was to determine whether nuthatch nest patch selection criteria changed during this outbreak, possibly due to a trade-off between patches with abundant nest trees versus foraging trees. If so, then we expected nest patch vegetation to have a greater density of live and dead aspen trees than do available patches (i.e., those containing  $\geq 1$  suitable-sized dead aspen nest tree) during preoutbreak years and a greater density of beetle-infected pine trees during outbreak years.

## STUDY AREA

The study area was located within the warm and dry Interior Douglas-fir biogeoclimatic zone, near Williams Lake, in central interior British Columbia (51°52'N, 122°21'W).

<sup>1</sup> E-mail: arnorris@interchange.ubc.ca

**Table 1.** Generalized linear mixed-effects model parameter estimates explaining variation in red-breasted nuthatch nest patch use to habitat variables in central British Columbia, Canada, during 1995–2005, with the following fixed effects: densities of aspen, mountain pine beetle–infected lodgepole pine, and suitable nest trees.

Time period	Parameter	Estimate	SE	df	<i>t</i>	<i>P</i>
Preoutbreak (1995–2002)	Intercept	−2.491	0.254	765	−9.809	<0.001
	Aspen	0.035	0.012	765	2.873	0.004
	Beetle-infected pine	0.029	0.050	765	0.569	0.569
	Suitable nest trees	0.090	0.032	765	2.776	0.006
Outbreak (2003–2005)	Intercept	−1.792	0.282	349	−6.352	<0.001
	Aspen	0.038	0.018	349	2.181	0.030
	Beetle-infected pine	0.090	0.032	349	2.756	0.006
	Suitable nest trees	0.010	0.060	349	0.166	0.868

Predominant tree species were interior Douglas-fir and lodgepole pine interspersed with patches of grassland and stands of quaking aspen (*Populus tremuloides*; Martin and Eadie 1999). The 27 sites were located within 40 km of Williams Lake and ranged from deciduous and coniferous forest stands (>30 ha) to small, isolated, natural forest fragments (0.1–5 ha) in a matrix of grassland, ponds, and wetlands.

## METHODS

Between May and July, 1995–2005, we conducted systematic searches for active nests on all sites, as well as checked old nest trees for reuse. We considered a nest active if we observed  $\geq 1$  egg or chick upon visual inspection of a cavity or if we observed an attending pair feeding nestlings. Each year, we collected vegetation data at all active nest patches and at systematically placed plots (representing availability) 100 m apart throughout all sites. We recorded tree species, diameter at breast height, decay class (decay class 1 was a live, healthy tree; 2, a live tree with visible sign of disease or decay such as bark-boring insects; 3–8 were standing dead trees; Thomas et al. 1979), and general health (e.g., presence of bark-boring insects) for all trees  $\geq 12.5$  cm diameter at breast height within an 11.3-m (0.04-ha)-radius circular plot centered around each nest tree or available plot. We detected mountain pine beetles on lodgepole pine trees by the presence of outflows of dried resin on the outer bark or by small bore holes (approx. 2 mm diam) in the bark. We determined density of beetle-infected pine by the number of lodgepole pine trees with evidence of bark-boring insects per hectare. Additional nest monitoring and vegetation survey methodology are given in Aitken et al. (2002) and Martin et al. (2004). We assumed that nuthatches were limited by nest tree availability so we chose all systematic vegetation plots in our study that contained  $\geq 1$  standing dead aspen tree that was within the observed diameter at breast height range of nest trees used by nuthatches on our sites (between 12.5 cm and 30.8 cm, hereafter suitable nest trees; Martin et al. 2004) and used these as our available patches ( $n = 1,136$  plots). We calculated densities of total aspen (live and dead trees/ha) and suitable nest trees (standing dead aspen trees/ha).

We used generalized linear mixed-effects models to determine whether nuthatch nest patches differed in tree species composition and condition from those available

before and during a mountain pine beetle outbreak. We converted the binary dependent data (used or available) into a logistic distribution using a logistic regression (logit) link function and used penalized quasi-likelihood ratios for parameter estimation (Breslow and Clayton 1993). Mixed-effects models allow the use of unbalanced and potentially pseudoreplicated data by splitting the within-group variation due to random effects from the between-group variation due to fixed effects (Pinheiro and Bates 2000). Fixed effects were density of aspen, density of suitable nest trees (standing dead aspen), and density of beetle-infected pine trees for each patch. We included site and year as random effects in all models to control for site-specific persistent effects (e.g., similar tree species composition and condition within sites or within-site variation due to harvesting) and potential pseudoreplication and unbalanced data across years due to multiple measurements of systematic plots and nest patches (e.g., some nest patches were used by nuthatches for multiple yr). We examined all 2-way interaction terms for each model constructed but none were significant, so we present only the most parsimonious univariate effects models. We constructed 2 separate models, based on the mountain pine beetle outbreak time period, to compare the relative contribution of each effect on nest patch selection between periods. The preoutbreak model included data from 1995 to 2002 and the outbreak model from 2003 to 2005. We conducted all statistical analyses using the program R (R Development Core Team 2006).

## RESULTS

We used data from 231 nest patches and 1,136 unused (available) patches to model the influence of aspen trees, suitable nest trees, and beetle-infected pine trees on nuthatch nest patch selection. Of the 231 nests examined in this study, 90% were located in aspen trees. As predicted, nuthatches selected patches with 44.3% higher mean densities of aspen trees than available in preoutbreak years (used = 316 trees/ha, SE = 24; available = 219 trees/ha, SE = 7), and 24.6% higher during the outbreak (used = 248 trees/ha, SE = 22; available = 199 trees/ha, SE = 11; Table 1). Nest patches had 63.5% higher mean densities of suitable aspen nest trees than available in preoutbreak years (used = 103 trees/ha, SE = 14; available = 63 trees/ha, SE = 2) but not in outbreak years (used = 69 trees/ha, SE = 6; available = 62 trees/ha, SE = 2; Fig. 1).

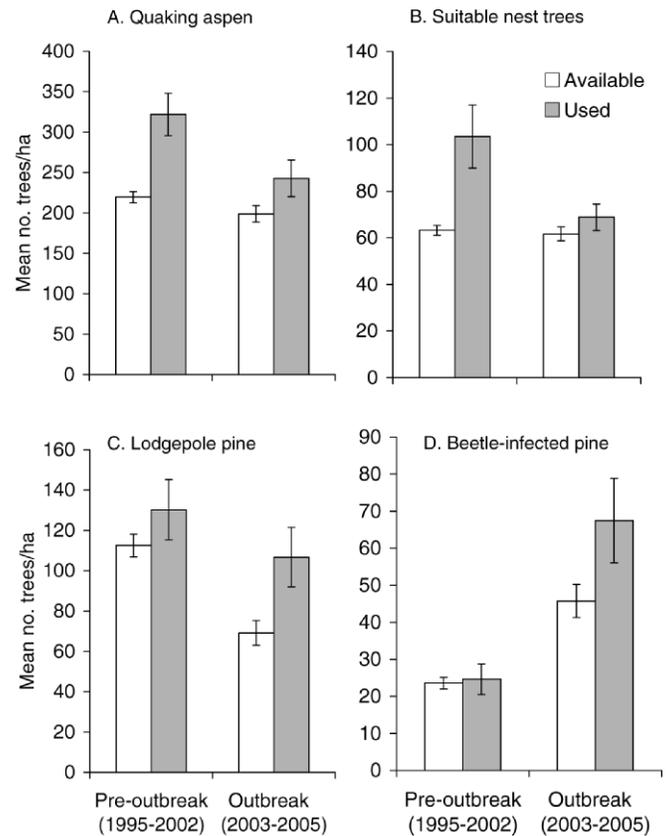
Mean density of beetle-infected pine trees among used (29 trees/ha, SE = 5) and available patches (24 trees/ha, SE = 2) did not differ prior to the outbreak (Fig. 1; Table 1). However, in outbreak years, nuthatches selected patches with 37.0% more beetle-infected pine trees than available (used = 63 trees/ha, SE = 11; available = 46 trees/ha, SE = 5).

## DISCUSSION

Nuthatches showed a strong preference for nest patches with high aspen densities, probably as a result of greater nest tree availability in these patches (Martin et al. 2004). Quaking aspen was the dominant deciduous tree species in the study area and exhibited both clumped and single-tree distribution, depending on the mode of reproduction (sexual vs. asexual; Callan 1998). In asexually reproducing aspen, the presence of one dead or decaying aspen tree often indicates that other trees in the aggregation are in the same condition, providing multiple nest trees within a single patch. We provide 3 possible explanations for our result that nest patches comprised higher densities of aspen and suitable nest trees in preoutbreak years (Fig. 1). First, nuthatches may have cued in to aggregated aspen because these patches would likely contain a suitable nest tree, thus minimizing time spent searching for a nest site. Nuthatches may have selected nest trees in patches because these were preferable to nesting in dispersed trees or low-density aspen patches for foraging or other activities. Lastly, nesting in patches with high densities of aspen and suitable nest trees may increase the probability of other cavity-nesters nesting nearby, increasing vigilance for predators in the area (Brown and Brown 1987, Soler and Soler 1996).

During outbreak years, nuthatches switched to nest patches with higher densities of beetle-infected pine trees, and lower densities of aspen, than those in preoutbreak years, which probably resulted in fewer suitable nest trees in patches. Thus, preference for both aspen and beetle-infected pine trees may have constrained nest patch selection.

Our data support the conclusions of previous studies that forest insect outbreaks contribute to habitat preference and nest patch choice of cavity-nesting birds (Morris et al. 1958, Crawford and Jennings 1989, Steeger and Hitchcock 1998, Conner et al. 1999). Patches containing high densities of aspen and beetle-infected pine were preferred over other suitable patches, possibly due to greater food availability. Although we did not examine the entire arthropod community, mountain pine beetles were likely the most prevalent insect available for bark-gleaning birds in our forest stands during the outbreak and may have constituted a significant portion of their diets, especially after 2001 (A. R. Norris, University of British Columbia, unpublished data). Nuthatches rely on adult beetles and larvae as a primary food source during the breeding season and over winter; beetles constituted 80% of nuthatch diets in ponderosa pine (*Pinus ponderosa*) forests and 64% in Douglas-fir forests during the breeding season in Oregon, USA (Anderson 1976). Food availability in aspen trees and other conifers may have been



**Figure 1.** Density of (A) quaking aspen, (B) suitable nest trees (standing dead aspen  $\geq 12.5$  cm dbh), (C) lodgepole pine, and (D) mountain pine beetle-infected lodgepole pine trees in patches containing  $\geq 1$  suitable nest tree (Available,  $n = 1,136$ ) and in red-breasted nuthatch nest patches (Used,  $n = 231$ ) for pre-outbreak and outbreak years, during 1995–2005, in central British Columbia, Canada. Error bars represent standard error of the mean.

higher than in pine trees prior to the outbreak, but the relative abundance of insects in those tree species declined with the beetle outbreak, precipitating stronger selection for pine patches. In early outbreak years, we found that nuthatches that nested in conifer-dominated stands fed their nestlings twice as often as those in aspen-dominated stands, suggesting a benefit of switching to nesting in these stands (A. R. Norris, unpublished data). However, our observation that nest patches prior to 2003 contained higher densities of pine than available indicates a general preference for patches with pine trees or mixed forest even before the beetle outbreak.

As year-round residents and bark insectivores, red-breasted nuthatches could be expected to show both numerical and functional responses to mountain pine beetle outbreaks (Morris et al. 1958, Crawford et al. 1990, Stone 1995). Mountain pine beetles provide nuthatches with increased food supply (developing larvae underneath bark in winter and emerging adults in summer), thereby potentially increasing survival and subsequent population densities. We found that nuthatch populations doubled and clutch sizes increased by approximately 30% with the peak of mountain pine beetle infection, which suggests that nuthatches may be able to predict summer food availability and select territories

accordingly, resulting in increased reproductive effort (Martin and Norris 2007, Norris 2007).

Although nuthatches showed immediate positive responses to mountain pine beetle outbreaks, later in the outbreak phase populations may decline due to increased mortality of pine and depletion of food resources. Red-breasted nuthatch abundance declined after 70% mortality of lodgepole pine stands caused by mountain pine beetle (Stone 1995). We found that nuthatch populations declined concurrently with declining beetle-infection rates in recent years, to levels below those in preoutbreak years, indicating a population collapse (Norris 2007). The positive response to the mountain pine beetle outbreak demonstrates that nuthatches will opportunistically exploit temporary changes in habitat conditions caused by forest insect outbreaks. However, increases in populations followed by sharp declines highlight the boom-and-bust trend associated with this ephemeral food source. Forest insect outbreaks are often accompanied by increased harvesting or targeted cutting of dead trees, thus imposing further constraints on nesting and foraging habitat and exacerbating the detrimental effects of diminishing habitat quality in postepidemic stands (Martin et al. 2006).

Weak cavity-nesters are limited by availability of nest trees and food, which are often linked because decayed trees offer both nest sites and foraging opportunities. Preference for aspen trees for nesting and conifer bark beetle-attacked trees for feeding presents a potential trade-off between selecting patches with better nesting habitat or foraging habitat. In mixed forests, red-breasted nuthatches can capitalize on bark beetle outbreaks because aspen trees are still available for nesting (albeit fewer), but foraging conditions are improved.

### Management Implications

In postepidemic conditions, there is a need to identify and retain refugia habitats for populations dispersing from areas of declining food availability. Red-breasted nuthatch is a conifer-associated species but requires aspen trees for nesting. To sustain cavity-nester populations in postepidemic conditions, managers should retain decaying and dead aspen, which offer nesting substrates, as well as healthy conifers and aspen, which offer potential future food and nest-site resources.

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