Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior: Implications for critical habitat management

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Abstract

The health of coniferous and mixed forests in western Canada is a critical forest management issue with implications for the forest industry, biodiversity conservation, and regional land use planning. The mixed forests of interior British Columbia have high biodiversity and species abundance, and support rich communities of over 185 wildlife vertebrate species, about 24% of which are cavity-nesters. These cavity-nesting birds and mammals live in complex, strongly structured wildlife communities (Nest Webs) that consist of an array of excavators and consumers of tree holes, many of which have strong preferences for large, old and decayed trees, especially deciduous trees, for nesting.

Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) and fire are the two major natural disturbance types structuring mature conifer stands in the interior of the province. The temporal changes in value and availability of dead and dying trees and their associated insect fauna are expected to result in stand-level variation in wildlife populations. Our research in the Cariboo-Chilcotin region showed that insect outbreaks can initially result in improved conditions for cavity-users and many other birds that feed on insects in dead and dying trees, but as the epidemic proceeds, these enhanced conditions deteriorate for many species as the supply of forest insects and old trees decline. The cumulative effects of habitat and environmental changes on the working landscape have the potential to negatively affect the stability of wildlife populations. This paper summarizes field observations regarding changes in forest stand conditions and avian biodiversity and evaluates the patterns of habitat change, beetle salvage, and wildlife responses as the MPB epidemic runs its course. It also discusses some of the issues that forest managers face when considering the maintenance of critical habitat for cavity-nesting species.

KEYWORDS: *avian beetle predators, biodiversity and forest health, cavity-nesting birds and mammals, critical habitat attributes, natural disturbance types, standing dead and unhealthy trees, variable retention.*

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Introduction

Insect epidemics and fire are the primary natural disturbance agents influencing the succession of pine ecosystems (Kilgore 1978; Schowalter *et al.* 1981). The current outbreak of mountain pine beetle (MPB; *Dendroctonus ponderosae*) is the largest ever recorded for the province and for North America. Facilitated by a series of mild winters, which resulted in low over-winter mortality of beetle larvae (Hughes and Drever 2001; Wood and Unger 1996), the outbreak has spread over 8.5 million ha of forests in the province, killing primarily lodgepole pine (*Pinus contorta* var. *latifolia*; Eng *et al.* 2005).

The mixed forests of interior British Columbia support rich communities of forest wildlife, including 171 species of birds (Drever and Martin 2007). In healthy and productive forest ecosystems, dead and dying trees provide critical nesting, roosting, and foraging resources for many wildlife species (Harmon *et al.* 1986; Harestad and Keisker 1989; Martin *et al.* 2004a). In the British Columbia interior, and in the Pacific Northwest generally, about 24–30% of forest vertebrate species are cavity-nesters, which nest or roost in tree cavities; a majority of these species do so exclusively (Bunnell *et al.* 1999; Drever and Martin 2007). Thus, natural and bird-excavated cavities become an important element for forest vertebrate biodiversity (Keisker 1987; Martin and Eadie 1999). Many of these cavity-nesting species cannot create their own cavities, depending instead on woodpeckers to produce them.

Martin and Eadie (1999) coined the term "Nest Web," analogous to a food web, to describe the hierarchical structure of cavity-nesting communities wherein species are classified into guilds according to the manner in which they acquire cavities. Woodpeckers, as primary cavity-nesters, excavate cavities in trees for nesting and roosting sites. Secondary cavity-nesters, which include a range of songbirds, ducks, birds of prey, and small mammals, depend on these cavities and on the less available natural tree holes. A third guild of small cavity-nesters is able to both excavate their own cavities and use naturally occurring holes as well as the cavities produced by woodpeckers (Martin *et al.* 2004a). Therefore, cavities in trees become a nesting and roosting resource for many forest species through a process that depends on the supply of dead and dying trees, as well as on other factors such as competition, predation, and facilitation among species in the community (Drever and Martin 2007).

Insect outbreaks may have significant effects on avian biodiversity, either directly by altering food availability or indirectly by altering habitat suitability for birds.

Insect outbreaks may have significant effects on avian biodiversity, either directly by altering food availability or indirectly by altering habitat suitability for birds. For example, many cavity-nesting species forage on dead and dying trees for insects, including bark beetles and defoliators (Bull *et al.* 1986). Pulses of food caused by conifer bark beetle and budworm outbreaks increase the food available for breeding birds (Otvos 1979) and thereby enhance the breeding success of these birds (Sillett *et al.* 2000). Bark beetle larvae are also a major food for woodpeckers in winter (Kroll and Fleet 1979). Thus, an increase in beetle densities may increase the population density, breeding success, and (or) winter survival of forest bird species. Insect outbreaks may also indirectly alter habitat suitability for birds. Woodpeckers, for example, prefer conifers as foraging sites when these trees are in advanced stages of decay; deciduous trees are preferred in early stages of decay (Bunnell *et al.* 2002). Since the value and availability of dead and dying trees and associated insect fauna depend on forest species composition and will change over time, stand-level variation is expected in responses of wildlife to changes in forest health. In addition, birds that feed on MPB may help to regulate bark beetle populations at endemic and post-epidemic levels (Otvos 1979; Steeger *et al.* 1998). For example, birds feed on bark beetles and also contribute to their death by thinning bark, dislodging beetle broods, and increasing opportunities for parasitism of beetle broods by other insects (Moore 1972; Kroll and Fleet 1979).

Mountain pine beetle epidemics remain an essentially unstudied natural disturbance type despite the regularity of insect outbreaks, the vast amounts of forest wildlife habitat involved, and the often-stated importance of ecosystem management and understanding natural disturbance regimes. A study of the post-epidemic effects of MPB on wildlife habitat and communities in lodgepole pine forests in northern Utah is a notable exception (Stone 1995).

The Nest Web project we conducted in the Cariboo-Chilcotin region of British Columbia provided an opportunity to examine the temporal changes in habitat that have resulted from large-scale tree mortality events due to bark beetles and other forest insects. Because our project began in 1995 before the bark beetle outbreak, we were able to track wildlife population shifts before and during this regional-level change in forest health and to determine the role of insect outbreaks on the community dynamics of cavity-nesters. We expected that interactions between bark beetle populations and cavity-nesting species would alter the Nest Web community. Most cavity-nesters are insectivores, so outbreaks of coniferous bark beetles likely represent an initial enhancement of habitat quality for foraging through increases in food supply. Therefore, populations of cavity-nesters should show significant increases in areas most heavily affected by bark beetles, and year-round residents should experience greater population increases than migratory species. As this epidemic proceeds, however, conditions are expected to deteriorate for many species as the supply of forest insects and old trees decline.

In this paper, we first describe our Cariboo-Chilcotin study area and then summarize our observations regarding changes in forest stand conditions and avian biodiversity as a result of the MPB outbreak. We conclude the paper with a discussion of several issues that forest managers face when considering the maintenance of critical habitat attributes for cavity-nesters and other forest species during and after the MPB epidemic.

The "Nest Web" Project: Study Area and Project Design

Our long-term field study area, located near Williams Lake, B.C., consists of mixed coniferous and deciduous mature forest embedded in a matrix of grassland and shallow ponds within the warm and dry Interior Douglas-fir (IDF) biogeoclimatic zone (Meidinger and Pojar 1991). Predominant tree species include lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), white and hybrid spruce (*Picea glauca × engelmannii*), and trembling aspen (*Populus tremuloides*). The majority of our 27 sampling sites were classified as the IDFdk3 (Fraser) or IDFxm (very dry mild) biogeoclimatic variants, with basal area values ranging from 24 to 39.6 m²/ha, although three sites were classified as the Sub-Boreal Pine–Spruce moist cool biogeoclimatic variant (SBPSmk). At the start of the study in 1995, all sites were mature forests (age class 8 and 9).

From 1995 to 2005, we monitored characteristics and conditions of trees and forest stands using standardized forest inventory, wildlife tree, and forest health monitoring techniques. This involved annual measurements in late summer of more than 10 000 individually marked trees. For all trees with a diameter at breast height (DBH) of 12.5 cm or more within our circular (11.3 m radius) vegetation plots, we recorded tree species, DBH, decay class (Thomas *et al.* 1979), condition (Finck *et al.* 1989), and other characteristics.

We located nests by systematic searches across sampling sites and recorded nest and tree characteristics. From 1995 to 2005, bird and squirrel populations were assessed during May and June using point-count (6 minutes of listening) and playback techniques. Table 1 lists the cavity-nesting species present in the study area (Martin *et al.* 2004a). See Martin and Eadie (1999), Aitken *et al.* (2002), and Martin *et al.* (2004b) for further details about the study area and project design.

TABLE 1. Cavity-nesting species present in the Cariboo-Chilcotin study area

Primary cavity-nesters	Secondary cavity-nesters
Woodpeckers	*Ducks*
Red-naped sapsucker	Wood duck
Hairy woodpecker	Common goldeneye
Three-toed woodpecker	Barrow's goldeneye
Black-backed woodpecker	Bufflehead
Northern flicker	Common merganser
Pileated woodpecker	Hooded merganser
Downy woodpecker	
	Insectivorous Birds
Weak Excavators	Vaux's swift
Red-breasted nuthatch	Tree swallow
Mountain chickadee	Violet-green swallow
Black-capped chickadee	European starling
Boreal chickadee	House wren
	Mountain bluebird
	Birds of Prey
	American kestrel
	Flammulated owl
	Northern pygmy owl
	Northern saw-whet owl
	Boreal owl
	Northern hawk owl
	Barred owl
	Great-horned owl
	Mammals
	9 possible species of bat
	Bushy-tailed woodrat
	Red squirrel
	Northern flying squirrel

Observed Changes in Forest Habitat and Avian Biodiversity in the Cariboo-Chilcotin Study

Changes to Mixed Coniferous Forest Habitat in Response to Bark Beetle Attack

Forest stand conditions in our study plots changed dramatically between 1995 and 2005. Although over 90% of the mature conifers were categorized as healthy in 1995, there was a steady decline to 45% healthy trees by 2005, accompanied by increases in unhealthy trees; in 2004, the number of dead trees increased sharply (Figure 1). These changes in tree health and mortality were correlated with increases in the proportion of beetle-attacked conifers from less than 2% in 1995 to 40% in 2005 (Figure 2). As expected, the intensity of bark-beetle attack was the highest for lodgepole pine, although all conifer species had increased levels of decay over time (Figure 2). Patterns of bark-beetle attack and consequent effects on tree health also showed considerable spatial variation. For example, in 2005, the proportion of beetle-attacked lodgepole pine across our study sites varied from 82 to 100%, with conifer tree mortality rates varying from 4.9 to 82.3% (11 uncut sites; K. Martin, unpublished data). This high degree of spatial variability in beetle-attack and tree mortality suggests that the severity of the outbreak will be highly heterogeneous at the landscape level, in a manner analogous to the effects of fire (Turner *et al.* 1994). These temporal and spatial patterns of heterogeneity of attack are likely critical to maintaining forest biodiversity.

Changes in Wildlife Population Trends in Response to Bark Beetle Outbreaks

Using point-count surveys, we found that 40% of 100 bird species experienced significant population changes over the past 11 years (Drever and Martin 2007). Although species richness and community-level abundance remained stable during the buildup of beetles to the peak in 2005, abundance trends for individual species were highly variable. For example, black-backed woodpeckers, three-toed woodpeckers, and downy woodpeckers—year-round residents feeding extensively on wood-boring beetle larvae (Dixon and Saab 2000; Leonard 2001; Jackson and Ouellet 2002)—all showed positive trends in abundance (Table 2; Drever and Martin 2007). Two of four small cavity-nesting species (mountain and boreal chickadees) also showed positive trends in abundance during the study (Table 2). In contrast, the migratory northern flickers and red-naped sapsuckers, which forage primarily on ants and tree sap (Moore 1995; Walters *et al.* 2002) decreased.

Densities of most resident cavity-nesting species increased over the study. For example, the mean density of nests located during standardized searches increased significantly for all of the resident woodpeckers except the pileated woodpecker (Figure 3a). Nest density of small-bodied cavity-nesters also increased through the decade except for black-capped chickadees (Figure 3b).

In other studies, the response of cavity-nesters to beetle outbreaks was not linear; that is, initial increases in populations were followed by steep declines (Conner *et al.* 2001).
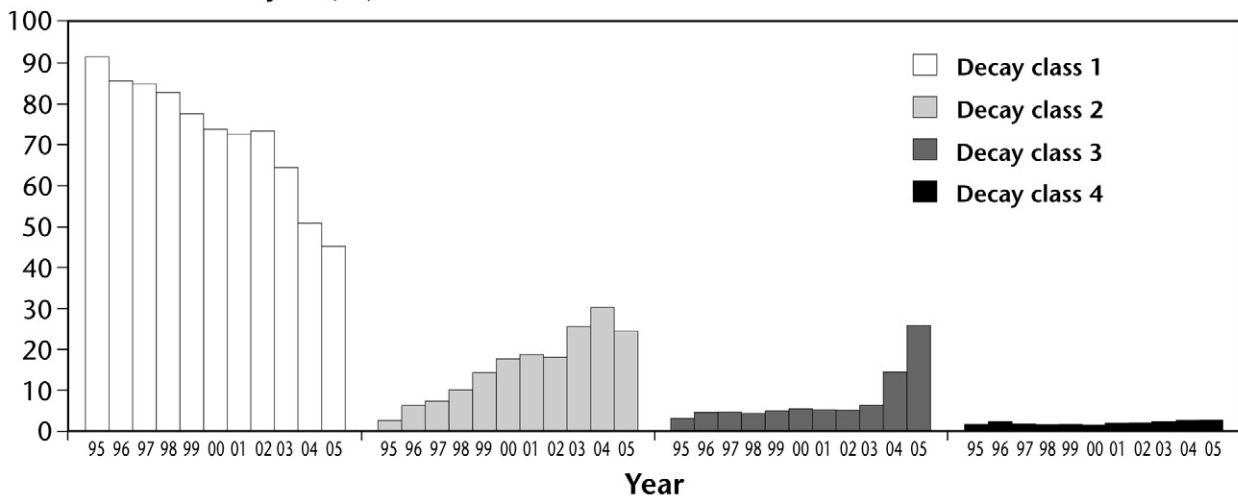
Conifer trees surveyed (%)

FIGURE 1. Temporal changes in the proportion of healthy (decay class 1), unhealthy (class 2), and recently dead conifers (classes 3 and 4) in the Cariboo-Chilcotin study area. Decay classes 5–8, which are not shown, remained virtually unchanged throughout the study; in 1995, these classes represented 1.3% of all trees and 1.9% in 2005.

Therefore, we looked for evidence of "boom and bust" trends in our study by focussing on the small-bodied cavity-nesters because their densities were high enough to allow an examination of population responses to the outbreak. Since this guild includes species that vary in whether they excavate their own cavities (e.g., mountain chickadees do not excavate, while red-breasted nuthatch and black-capped chickadees do excavate), we were able to explore how bird population responses differed depending on whether they were limited only by the availability of food or also by the availability of nest sites.

In the Cariboo-Chilcotin region of British Columbia, mountain chickadees are year-round residents that occupy stands of mixed coniferous-deciduous forest,
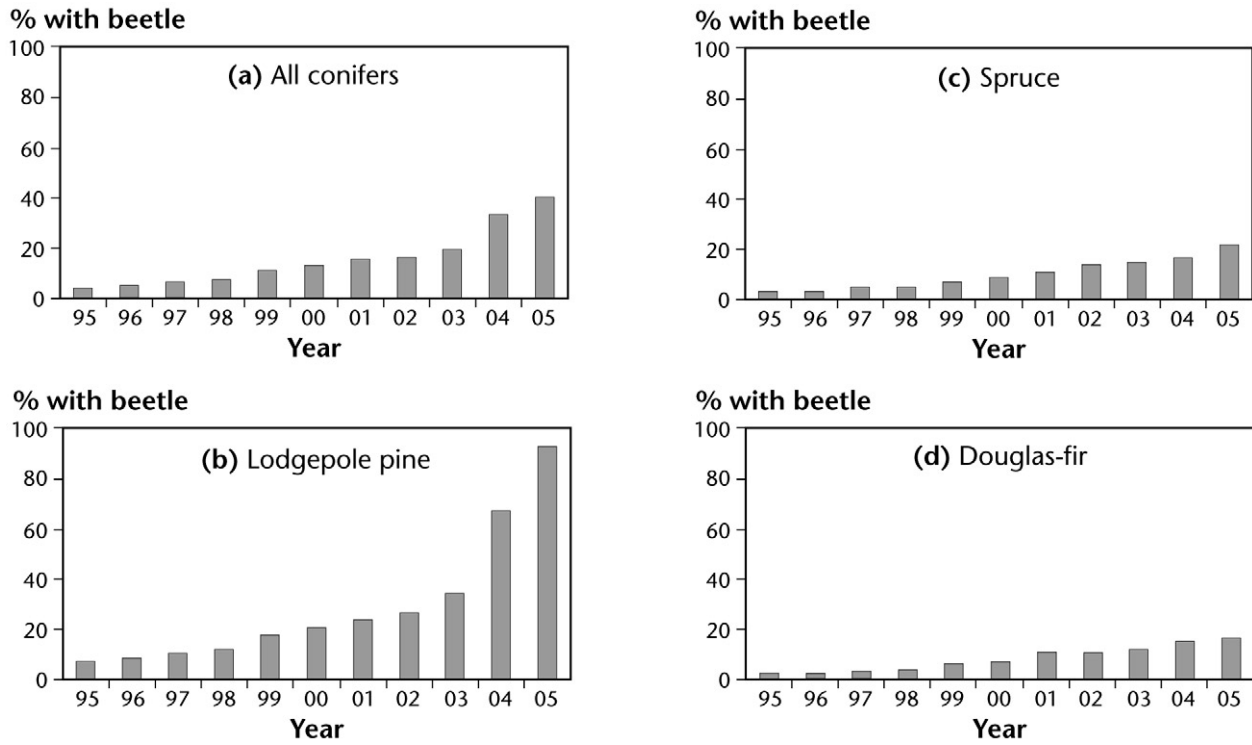
FIGURE 2. Prevalence of bark beetle attack over 11 years in the Cariboo-Chilcotin study area: (a) all conifers; (b) lodgepole pine; (c) spruce; and (d) Douglas-fir.
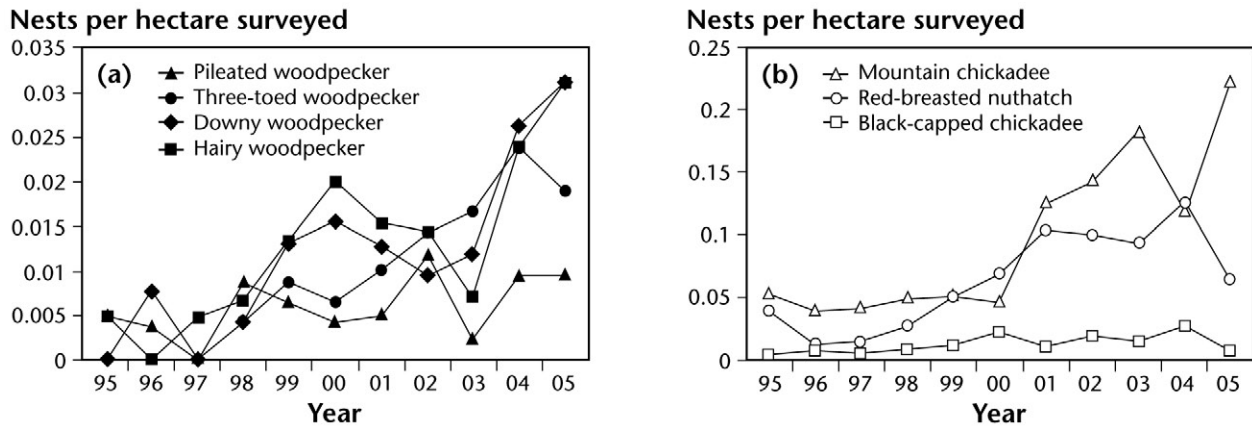

FIGURE 3. Mean nest density of resident cavity-nester species over 11 years: (a) woodpeckers; and (b) small-bodied cavity-nesters.

especially Douglas-fir, pine, and aspen (Martin and Norris 2007). They are the most abundant small-bodied cavity-nester breeding at our study sites. Detection rates using point counts doubled between 1995 and 2004 (from 1.5 to 3 detections per 10 ha) and their nesting density tripled since 2001 (Figure 3b; Martin and Norris 2007). Mountain chickadees used holes excavated by red-naped sapsuckers (40% of 163 cavities), red-breasted nuthatches (23%), and downy woodpeckers (17%), as well as natural holes (11%; Martin and Norris 2007).

The red-breasted nuthatch, a species of similar size and weight to the chickadee (~10–11 g), excavates about 50% of its nests and prefers coniferous habitat (fir and spruce forests) similar to mountain chickadees

(Ghalambor and Martin 1999). Early in the beetle outbreak, nuthatches showed almost linear annual increases that corresponded with increased beetle-attack on conifers until 2003. After 2003, pooled data from two areas (Likely Road and Stack Valley Road) showed strong spatial variation in nuthatch trends despite similar continued increases in the proportion of conifers with bark beetle attack to about 50% in 2005 (Figure 4). At our Likely Road study site, nesting densities sharply increased from 1998 to 2004, and then levelled as the proportion of conifers with beetle-attack continued to increase from 40 to 50%. In contrast, nuthatch nesting densities at the Stack Valley Road site declined by 80% over the last 3 years to about 2 nests per

TABLE 2. The beetle eaters: Bird and mammal species present in the Cariboo-Chilcotin study area that eat conifer bark beetle larvae and adults

Species	Migratory status[a]	Population status[b]	Stage eaten[c]	Reference
Red-naped sapsucker	M	↓		Yellow-bellied sapsucker (Kroll and Fleet 1979)
Hairy woodpecker	R	nc	L, A	References in Steeger *et al.* 1998
Three-toed woodpecker	R	↑	L, A	References in Steeger *et al.* 1998
Downy woodpecker	R	↑	L, A	References in Steeger *et al.* 1998
Black-backed woodpecker	R	↑	L, A	Lester 1980
Northern flicker	M	↓		Kroll and Fleet 1979
Pileated woodpecker	R	nc	L, A	References in Steeger *et al.* 1998
Olive-sided flycatcher	M	↓	A	Otvos 1979
Western wood-peewee	M	↓	A	Otvos 1979
Pacific-slope flycatcher	M	nc	A	References in Steeger *et al.* 1998
Tree swallow	M	nc	A	References in Steeger *et al.* 1998
Violet-green swallow	M	nc	A	Otvos 1969, 1970
Black-capped chickadee	R	nc	L, A	Unpublished data; references in Steeger *et al.* 1998
Mountain chickadee	R	↑	L, A	Baldwin 1968
Chestnut-backed chickadee	R	?		References in Steeger *et al.* 1998
Boreal chickadee	R	↑	L, A	References in Steeger *et al.* 1998
Red-breasted nuthatch	R	nc	L, A	References in Steeger *et al.* 1998
Brown creeper	R	↑	L, A	References in Steeger *et al.* 1998
Mountain bluebird	M	↑	A	Baldwin 1968
American robin	M	nc	A	Otvos 1979
Yellow-rumped warbler	M	↓	A	Forbush 1929
Western tanager	M	nc	A	Otvos 1979
Dark-eyed junco	M	↑	A	Otvos 1979
Red squirrel	R	↓	L	Goodman 2004

[a] Migratory status: M = migratory; R = resident.

[b] Trends in population abundance based on point count data from uncut sites, 1995–2005 are scored as: ↑ = significant increase; ↓ = significant decrease; nc = no change; ? = unknown (Drever and Martin 2007).
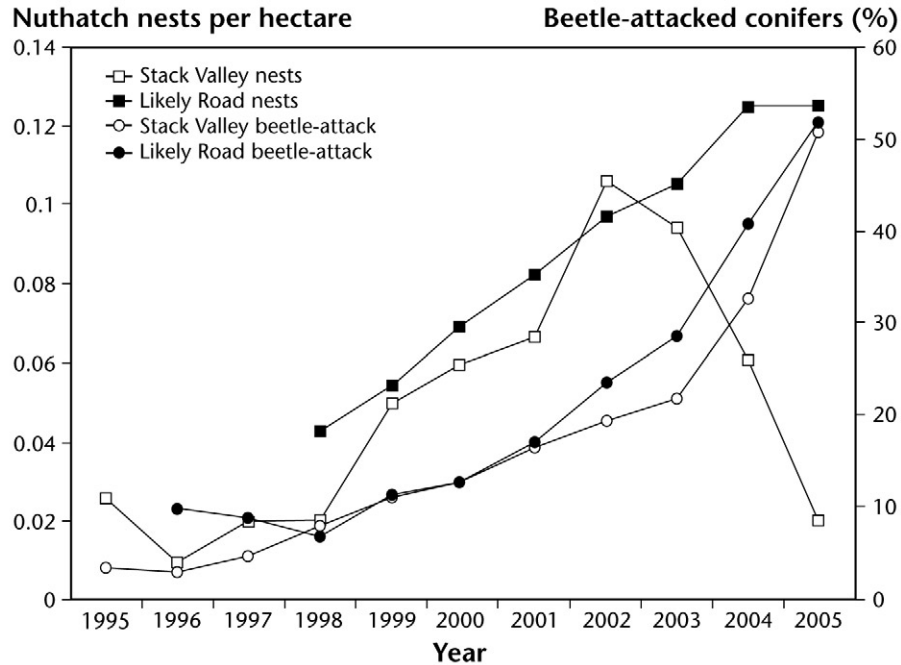
[c] Stage eaten: L = larvae; A = adult.

FIGURE 4. Trends in the density of red-breasted nuthatch nests and the proportion of beetle-attacked conifers at two study-site clusters (Stack Valley, Likely Road) in the Cariboo-Chilcotin.

100 ha in 2005 (Figure 4). Breeding bird surveys in British Columbia showed an overall increase in red-breasted nuthatches from 1995 to 2004 (Sauer *et al*. 2005). In 2005, nuthatches returned to the pre-outbreak levels of 1995–1998 at the Stack Valley Road site and in the study area as a whole (Figures 3 and 4). However, these birds are returning to radically altered forest conditions compared to their pre-outbreak habitats.

Beetles in the Nest Web: Effects of Bark Beetle Outbreaks on Avian Biodiversity

Interior Forest Habitats: Rates of Change and Uncertain Outcomes

The insect outbreak in the interior of British Columbia has been accompanied by many other environmental changes and forest management activities, creating uncertain outcomes in wildlife communities. Since 1997, bark beetles have attacked all conifer species, with MPB being the most abundant on lodgepole pine, the dominant tree species. The MPB outbreak has resulted in a large increase in the availability of dead and dying conifers, an important foraging resource for many wildlife species in interior forests. There has also been a significant loss of mature forest in the region.

During the past decade, we observed high annual variability in abundance of individuals at both the species and site levels (Drever and Martin 2007). For the small-bodied cavity-nesting species (with smaller territories), such as the mountain chickadee, we were able to monitor population change. Using population growth models, we determined that the critical drivers in mountain chickadee demography were density dependence, beetle abundance, density of trees, and woodpecker density. Furthermore, the negative density-dependent effects were strongly ameliorated with high beetle abundance (Martin and Norris 2007). Thus, mountain chickadee population densities depend on food availability and density of facilitator species to excavate their nest holes. Although we found similar positive effects for nuthatches up to 2003, we have since noted a strong population decline. In 2006, both species were at very low densities at all of our study sites (K. Martin and A.R. Norris, unpublished data). Given the similar population responses to insect outbreaks by these two small cavity-nesters, excavation ability does not appear to be an important explanatory factor.

A study on avian densities in post-epidemic MPB-attacked lodgepole pine forests of northern Utah found that species diversity and abundance for all birds, and also for most groups of birds, increased to a peak in

stands with up to 60% tree mortality, and thereafter showed steep declines with tree mortality of 70–100% (Stone 1995). In the mixed forests of our study area, avian declines may also be occurring as conifer mortality exceeds 50% (Figure 5); however, it may be premature to compare our results with Stone (1995) as conifer mortality has exceeded 60% in only two of our site-year combinations.

The Possible Role of Forest Birds in Biological Control of Beetles

The role of forest vertebrates in modulating forest insect outbreaks (Steeger *et al*. 1998) is still unknown because of the difficulties associated with obtaining information about the number and effects of beetle-eating vertebrates in most forests. Combining a literature search with our observations of species known to occur in the British Columbia interior, we estimate that a minimum of 24 species of birds and mammals consume conifer bark beetle larvae and (or) adults (Table 2).

The potential for insectivorous birds to contain beetle infestations is uncertain, particularly during major outbreaks; however, given the diversity of birds that forage on bark beetles, a significant depression in beetle population dynamics may be possible. For example, when spruce bark beetle populations were at moderate to high levels, woodpeckers ate or otherwise destroyed 24–98% of beetles (Otvos 1979). Some birds feed on adult MPB during flight before these beetles can infect the next generation of trees (Dickson *et al*. 1979). If resident cavity-nesters generally show the functional and (or) numerical responses to bark beetle outbreaks that we observed in the Cariboo-Chilcotin, the increased predation pressure on beetles may have an influence on

> *Cavity-nesters may moderate the onset, distribution, duration, or intensity of pine beetle outbreaks.*

outbreak dynamics, especially by accelerating the decline after the peak of the outbreak. Given the intensity of the current pine beetle outbreaks in the British Columbia interior, cavity-nesting birds are unlikely to contain further outbreaks. Instead, cavity-nesters may moderate the onset, distribution, duration, or intensity of the outbreaks through delays to the onset of an outbreak or through a hastening of its decline. Even a reduction in tree mortality of 5–10% would be significant given the predicted mortality of 90 million m^3 of merchantable timber in the British Columbia interior (Eng *et al*. 2005).

Many vertebrate bark beetle predators are year-round residents and mature forest associates (e.g., large dead or decaying trees with cavities), and may show negative responses to aggressive beetle management. Therefore, a critical management concern for the long-term health of forests is to maintain roosting, nesting, and feeding habitats required by these beetle predators. The cavity-nesters in our study area showed strong preferences for specific habitat types and conditions when choosing nest trees and cavities. For example, most woodpeckers, nuthatches, and chickadees nest in aspen but feed on invertebrates that live in conifers. Several of the most important preferences are presented in the adjacent sidebar (see "Good nesting trees and tree holes: Cavity-nesting birds use large unhealthy and dead aspen for nesting" on page 18).
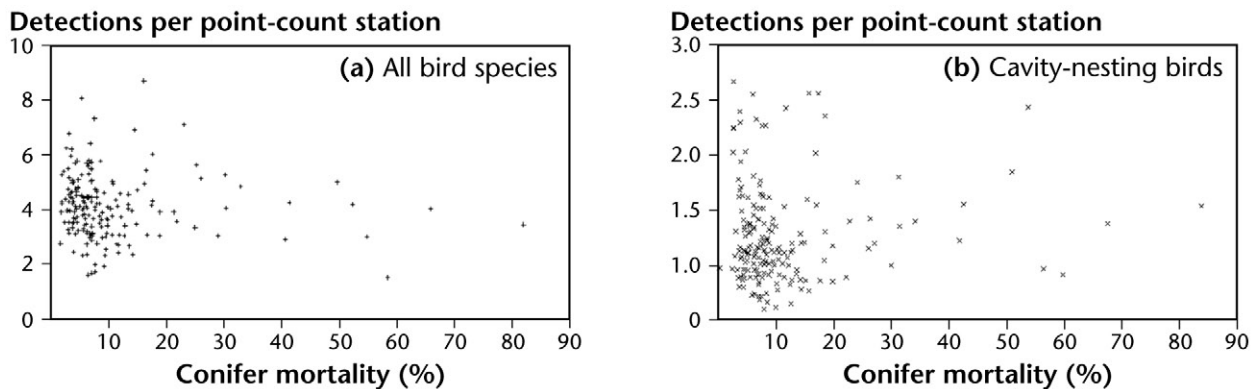

FIGURE 5. Avian detections per point-count station in relation to percent mortality of conifer trees, 1995–2005. Each symbol represents a site-year combination. Data are presented only for uncut or pre-cut sites: (a) all bird species; and (b) cavity-nesting birds.

Good Nesting Trees and Tree Holes: Cavity-nesting Birds Use Large, Unhealthy, or Dead Aspen For Nesting

Aspen accounts for only 15% of the trees over 12.5 cm diameter at breast height on our mature and old forest sites, but 96% of 2914 cavity nests were located in aspen (Figure 6; Martin *et al.* 2004a; 2003–2005 unpublished field data). Large trees were preferred, and although the full range of decay classes was used, birds showed a strong preference for live unhealthy (48% of nests) and dead trees (45%) for nesting (Figure 7; Martin *et al.* 2004a). The cavities most preferred by nesting birds:

- had an opening slightly larger than the body size of the bird;
- were 25–40 cm deep; and
- were generally located low on the tree (average height of 4–5 m) (Figure 8; Aitken *et al.* 2002; Martin *et al.* 2004a).

Although cavity-nesters will use holes in trees with multiple cavities and in very decayed trees, they strongly prefer to use live, unhealthy trees with only one cavity (Aitken and Martin 2004). Forest managers are accustomed to guidelines about retaining snags for nesting, roosting, and foraging by wildlife. Our studies highlight the importance of retaining live, unhealthy trees as these are strongly preferred by cavity-nesting birds. In addition, cavity-nesting species live in highly structured Nest Web communities, with trembling aspen as the most important nesting tree and northern flickers as the primary excavators (Martin *et al.* 2004a). Management practices that retain good numbers and distribution of these two keystone species will also safeguard other members of the Nest Web community.

FIGURE 6. Characteristics for a good nest tree for cavity-nesters.

FIGURE 7. Cavity-nesters strongly prefer unhealthy and dead aspen trees for nesting sites (ranks 1–3). "Percent used" is the percentage of each decay class (of a total of 769 aspen) used for nesting compared to the aspen trees available for use (*n* = 1246). Decay class codes from Thomas *et al.* 1979: class 1 indicates a live and healthy tree; class 2 indicates a live tree with visible signs of decay, and classes 3–8 indicate dead trees with advancing stages of decay. Rank refers to the difference between the percent used and available (rank of 1 indicates the strongest preference); although aspen of decay class 4 are the most strongly preferred, aspen of decay class 2 are the most important because they are more abundant.
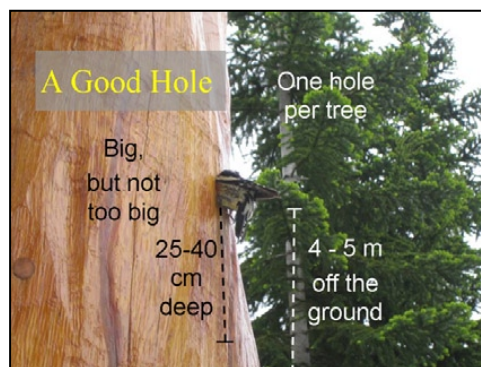

FIGURE 8. Characteristics for a good nest cavity: an entrance size that provides a snug fit for the body of the cavity-nester.

Cumulative Effects and Stressors Will Delay Recovery of Wildlife Habitats

The amount of mature lodgepole pine in this region has tripled since 1910, and most of this is currently vulnerable to attack from bark beetles and other forest insects (Taylor and Carroll 2004). However, the recovery of forests in the British Columbia interior is not just a matter of forest regeneration after the beetle outbreak. Many other agents of disturbance and change are active on the landscape. In addition to the declines in forest health, forest habitats and their associated wildlife species must also cope with the cumulative effects of multiple stressors. For example, the central interior of British Columbia is experiencing strong climate warming. In the past century, average minimum temperatures have increased by 2.6°C in winter, 2.2°C in spring, and 1.5°C in summer (British Columbia Ministry of Water, Land and Air Protection 2002). Beetle management activities, including extensive salvage of dead trees and pre-emptive cutting of live-attacked trees and pheromone-baited trees, have resulted in a significant increase in the allowable annual cut (tripled in some areas) (Taylor and Carroll 2004; B.C. Ministry of Forests and Range 2006). The widespread fire suppression activities in this area will also slow the removal of dead trees and forest regeneration on these cold, dry landscapes. Defoliating insects can hinder cone production and seedling recruitment and increase tree susceptibility to various pathogens, further altering forest structure across landscapes (Hadley 1994). Our ability to evaluate or predict the impacts of these massive habitat changes and the cumulative stressors on wildlife populations is strongly hampered by the almost complete lack of research activity on these problems. Yet, we need to manage for both biodiversity maintenance and forest regeneration despite the chaotic regime of ecosystem change.

Wildlife Population Trends During Epidemic and Post-Epidemic Conditions

What patterns of habitat change and wildlife responses can we expect as the bark beetle epidemic runs its course? The area affected by the MPB outbreak continues to expand and is predicted to peak in the summer of 2007 (Eng *et al*. 2005). To control the outbreak and salvage dead timber, more than 14 million m³ of live pine were planned for harvest in 2006. By the end of 2006, approximately 40% of the susceptible pine trees will be dead or harvested (Eng *et al*. 2005). In the midst of these epidemic and post-epidemic conditions, we need to determine key relationships between beetle-caused tree mortality and important animal community parameters, such as diversity, abundance, and occurrence, and predict future conditions for wildlife.

In the United States, woodpeckers showed a "boom and bust" relationship with the southern pine beetle (Conner *et al*. 2001). Woodpecker densities were shown initially to increase with beetle abundance in this study, then declined sharply as beetles ran out of susceptible trees. In pure lodgepole stands in Utah, a similar peak and decline was observed for birds and other vertebrate and invertebrate taxa after tree mortality exceeded 60% (Stone 1995). This latter study was exceptional in that it set out to measure post-epidemic changes in wildlife habitat quality due to MPB attack on stands with tree mortality ranging from 14 to 95%. The limitations of this study were that stands were only 1 ha in size and no pre-outbreak wildlife occurrence data existed; however, despite the small study stands, the pattern of boom and bust was quite strong across space and time.

In our study, the abundance of most resident cavity-nesters increased with increasing bark beetle attack. In 2005, however, we noted decreases in nuthatch and chickadee densities as the proportion of beetle-attack exceeded 40%; this indicates possible declines in habitat quality at some sites (Figure 3). Given the host of insect fauna associated with a bark beetle outbreak, it is not clear how to determine when the food disappears for a particular bird species. We are currently investigating the timing (critical season may be winter or summer) and the important mechanisms (loss of food or other limiting factors) behind these avian declines.

Post-Epidemic Conditions: Implications for Critical Habitat Management

Over the past 5 years, extensive salvage cutting has occurred around many of our study sites, such that some of our sites now represent the only remnants of old forest in the area (e.g., the Likely Road sampling sites). In the Interior Cedar–Hemlock (ICH) forests of the Hazelton-Kispiox region, higher breeding densities of chestnut-backed chickadees were associated with older forest and not partial harvest levels (30–60% volume removal) (Mahon 2006, Mahon *et al*. 2007; see adjacent sidebar, "Cavity-users require patches of old forest with decaying and dead trees" on page 20). Salvage or other cutting activities often do not negatively affect cavity-nesters and other forest vertebrates, especially at the beginning of forestry activities. Many forest species include some edge environments in their territories (Aitken *et al*. 2002;

Cavity-users Require Patches of Old Forest With Decaying and Dead Trees

Nest site limitation may be important for cavity-users in managed forests where suitable wildlife trees (dying or dead trees) are often removed to meet safety requirements for forest workers (Zarnowitz and Manuwal 1985; Hunter 1990; Steeger and Hitchcock 1998). Like other small-bodied cavity-excavators, chestnut-backed chickadees require decaying wood found in diseased, damaged, or dead trees with soft heartwood, to excavate nest cavities or to renovate existing natural or previously excavated cavities (Figure 9; Dahlsten *et al.* 2002). In northwest British Columbia, the abundance of chestnut-backed chickadees did not differ in uncut and partial-cut forests with 30% and 60% volume removal (Steventon *et al.* 1998; Mahon 2006). However, in both uncut and partial-cut stands, chickadees selected nest patches with more tree cover and higher densities of broken-top trees when compared to available habitat within their territories; for nesting, they selected large trees with insect-attack and broken tops (Mahon *et al.* 2007). Thus, chestnut-backed chickadees displayed good resistance to habitat change (i.e., they maintained breeding densities and tolerated habitat loss of up to 60% tree volume removal) in old and mature forests. Managed stands that maintain a variety of tree species and conditions, including live trees with disease, insect-attack, and physical damage, provided sufficient critical attributes for nesting by small cavity-nesters such as chestnut-backed chickadees (Figure 10; Mahon 2006; Mahon *et al.* 2007). The quality of habitat attributes remaining after forest management activities is therefore critical knowledge for the maintenance of wildlife biodiversity. Forest managers need to retain patches of live and dead trees that will remain standing after harvest.

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FIGURE 9. Mountain chickadee in nest cavity.

FIGURE 10. Critical habitat for cavity-nesters.

Mahon 2006). The increased light and open space near forest edges can provide favourable habitat for various shade-intolerant invertebrate species (Chen *et al.* 1992). However, many forest vertebrates also show a strong preference for large, old trees with decay which provide both foraging and nesting opportunities. Therefore, the effects of beetle salvage on bird communities and species will ultimately reflect the scale of forest management and the proportion of old forest attributes that remain, with modest or no effects evident until old forest remnants become small and isolated.

Given the spatial scale of this MPB outbreak and the high levels of wildlife diversity supported by forest ecosystems in the British Columbia interior, forest management options need to balance the priorities of biodiversity conservation and forest harvest and regeneration. To achieve this balance and provide essential management information, empirical studies are urgently needed about the effects of coniferous bark beetles (as a disturbance type) on wildlife communities and their habitats.

To integrate biodiversity values with silvicultural considerations when dealing with epidemic and post-epidemic salvage operations, forest managers must retain important wildlife habitat attributes on the landscape today and over the next 50 years. Maintaining healthy populations of forest vertebrates will almost certainly involve a network of old forest remnants with unhealthy and healthy large trees and a range of tree species. For example, a study in the Sicamous Creek Research Forest showed that retention of old forest patches in Engelmann Spruce–Subalpine Fir zone forests was better than individual-tree selection for maintaining avian species associated with mature conifers when 30% volume was removed in a first-pass cut (Leupin *et al.* 2004). We need to provide sufficient year-round foraging and nesting resources for the keystone species in wildlife communities, and to safeguard ecological processes such as tree regeneration against drought and other stochastic environmental parameters. Temporal requirements for maintaining old forest networks involve spreading the salvage activities over time across the landscape, a feasible option given recent estimates of shelf life for the commercial quality of the wood that allow protracted salvage activities (Lewis and Hartley 2006). We recommend the following considerations to maintain wildlife species in post-epidemic MPB conditions:

- Retain all possible aspen and other deciduous trees (keep all dead and dying trees), preferably in patches with conifers.

To integrate biodiversity values with silvicultural considerations when dealing with epidemic and post-epidemic salvage operations, forest managers must retain important wildlife habitat attributes on the landscape today and over the next 50 years.

- Retention patches should be a minimum of 1 ha, and include a few larger patches (> 10–50 ha) for mature-forest-dependent species; size of retention patches should increase with decreased proportion of old forest on the landscape.
- In post-epidemic conditions, riparian areas and other conifer forests will serve as wildlife refuges.

We will continue to examine the effects of bark beetle densities and habitat change throughout the outbreak to determine when sufficient resources are available to maintain wildlife populations on the working landscape after beetle-attack and beetle management activities.

Acknowledgements

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Test Your Knowledge . . .

Effects of bark beetle outbreaks on avian biodiversity in the British Columbia interior:
Implications for critical habitat management

How well can you recall some of the main messages in the preceding Discussion Paper?
Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. How many of the bird species and cavity-nesting mammals living in the Cariboo-Chilcotin region eat or kill conifer bark beetle larvae and (or) adults?
    A) 5
    B) 10
    C) 24

2. How have resident forest bird populations responded to the mountain pine beetle outbreak in the interior of British Columbia?
    A) No change
    B) Populations have increased, given more food and warm winters
    C) Boom and bust: populations initially increased then decreased sharply, but where is the bottom?

3. Bark beetle and other forest insect outbreaks are one of two major natural disturbance agents affecting mature conifer stands in the British Columbia interior, as well as the rest of continental North America. What is the second natural disturbance type?
    A) Fire
    B) Wind
    C) Hurricanes

4. What is the resource that structures Nest Web communities?
    A) Bark beetles
    B) Tree holes for nesting and roosting
    C) Predators

5. Bonus Question: I am a mustelid kit born in an old pileated woodpecker cavity 8.3 m high in an aspen, the first nest found of my species in over 3180 cavity nests in the Nest Web project. What species am I?
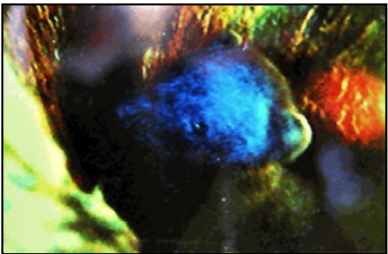
Christine Kent

    A) Fisher
    B) Pine marten
    C) Mink

ANSWERS

1. C 2. C 3. A 4. B 5. A