

A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest management

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Abstract

The mountain pine beetle epidemic has dramatically altered lodgepole pine forests in British Columbia, with potentially profound effects on wildlife and wildlife habitats. Forest managers should understand the nature of these effects so that they can incorporate ecological considerations when managing stands after beetle attack. This paper summarizes the processes by which the mountain pine beetle affect wildlife and wildlife habitats, and the factors that dictate the nature of these effects. Factors that affect the ecological legacy of unharvested, beetle-attacked stands include time since infestation, the type and amount of remaining live vegetation, ecosystem type, and surrounding landscape characteristics.

KEYWORDS: *ecological legacy, mountain pine beetle, sustainable forest management, unsalvaged mountain pine beetle stands, wildlife.*

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Introduction

The mountain pine beetle (MPB) epidemic has altered lodgepole pine forests to an unprecedented scale in British Columbia (Safranyik and Wilson 2006), with potentially profound effects on wildlife and wildlife habitats. Forest managers need to understand the nature of these effects so that they can balance economic and ecological considerations when making decisions about the manner and extent of salvage logging. Beetle-killed stands must be logged before the dead trees deteriorate to an unmerchantable condition (Pedersen 2004), but this need cannot preclude conservation strategies aimed at sustaining biodiversity in a massively defoliated landscape.

Although the effects of large-scale salvage logging have been previously addressed (e.g., Bunnell *et al.* 2004; Chan-McLeod and Bunnell 2004), little or no attention has been paid to the ecological legacy of unharvested stands. Managers critically require more information about the effects of unsalvaged MPB stands on wildlife and wildlife habitats, but few studies have addressed these issues. Moreover, past studies that did directly evaluate the effects of the MPB on wildlife date back to previous smaller-scale epidemics, which are of limited applicability to the current situation (e.g., Bull 1983; Steeger and Hitchcock 1998). The current epidemic has spawned considerable research on the effects of MPB on wildlife; however, much of this work is nascent and conclusions are still pending.

Given the urgency with which forest managers must now make decisions on where to focus salvage logging, immediate guidance can be drawn from our substantial knowledge of the natural history of the native fauna, including strong and well-defined relationships between forest structure and the occurrence and abundance of wildlife species (Thomas

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1979). The beetles have no direct effects on wildlife other than as a food source for some species. Rather, their effects are mediated through the forest structure, which represents the habitat for wildlife. Until new research findings are available, consideration of wildlife–habitat relationships can provide forest managers with the conservation perspectives they need to evaluate the ecological legacy of MPB-infested stands. To this end, this paper summarizes both the processes by which the MPB affect wildlife and wildlife habitats and the factors that dictate the nature of these effects.

Processes By Which the Mountain Pine Beetle Affect Wildlife

Mountain Pine Beetle as a Food Source

The MPB is an important food source for many avian vertebrates including the brown creeper, red-breasted nuthatch, northern flicker, three-toed woodpecker, black-backed woodpecker, hairy woodpecker, and olive-sided flycatcher (Koplin 1969; Bull 1983; Amman 1984; Bergvinson and Borden 1992; Steeger and Dulisse 1997). It is an especially critical food supply for the three-toed woodpecker and the black-backed woodpecker, which prey almost exclusively on bark beetles and wood borers (Steeger and Dulisse 1997; Fayt 2003), and which must move between fire- or beetle-killed areas to thrive (Hutto 1995). Other woodpecker species, though less dependent on the MPB, are nonetheless efficient predators that may play a significant role in regulating beetle populations under endemic situations (Amman 1984; Fayt *et al.* 2005). Several studies have documented an increase in woodpecker populations in response to an increase in food supply from beetle outbreaks (Baldwin 1960; Koplin 1969). When woodpeckers have not responded numerically to an increase in bark beetles, this is probably because population growth is limited by non-food factors such as the supply of nest sites (Fayt *et al.* 2005).

Bark beetles are an ephemeral food source because their successful colonization of a host tree depends on the death of that tree (Carroll and Safranyik 2004). An individual lodgepole pine serves as a brood tree for approximately 1 year (Safranyik 1978), which is a typical life cycle for mountain pine beetles in British Columbia. When beetles emerge in mid- to late summer, they will fly off and seek new living hosts, and the dead tree will no longer harbour any bark beetles. Thus, the nature of the infestation will dictate the length of time that a particular forest stand will provide an abundant food supply. If the infestation rate is extremely high, and all lodgepole pine are successfully colonized in one massive wave, then the forest stand will offer an abundant food supply for insectivorous birds for only 1 year. Conversely, if the first invasion by the MPB attacks a limited number of lodgepole pine, then the forest stand may represent an abundant supply of beetle prey for as long as brood trees exist in the stand. Collins *et al.* (1999) documented the transient response of woodpeckers to an ephemeral beetle food source. They found that three-toed woodpecker became more abundant after an outbreak of spruce bark beetle, but that populations declined when the infestation subsided and the availability of beetle larvae decreased.

Defoliation of the Tree Canopy

The eventual defoliation of beetle-killed trees will have major effects on wildlife species for several reasons.

1. Lodgepole pine needles are consumed by species such as the snowshoe hare (Sullivan and Sullivan 1988) and the blue and spruce grouse (Zwickel and Bendell 1970; Pendergast and Boag 1971; Hohf *et al.* 1987; Remington and Hoffman 1996).
2. The tree canopy supports invertebrates that are important to wildlife. Many bird species, including various chickadees, crossbills, kinglets, vireos, and warblers, feed primarily by gleaning insects from the foliage (Ehrlich *et al.* 1988).
3. The tree canopy is a resting or nesting habitat for both avian and mammalian species (Snyder and Cassel 1951; Campbell *et al.* 1997; Campbell *et al.* 2001; Smith *et al.* 2004; Nagorsen 2005).
4. The tree canopy provides shelter from inclement weather, as well as hiding and escape cover for prey species and hunting cover for predator species.

The elimination of cover is arguably the gravest consequence of tree defoliation, with implications for a broad spectrum of taxa including birds, small mammals, ungulates, furbearers, and medium and large

carnivores (Raphael 1989; Lyon *et al.* 1994; Smith *et al.* 2000). Elimination of cover affects wildlife not just at the localized, forest-stand level where they occur, but also at the large-scale, landscape level (Harris 1984; Voller and Harrison 1998). The continuity of suitable habitat (including cover) across the landscape dictates where animals can or will move to when searching for food or for mates. It also governs the probability of success for juveniles dispersing from natal areas and seeking to establish themselves in new territories, the migration of both adults and juveniles between seasonal habitats, and the interbreeding of sub-populations. The discontinuity of suitable habitat, or fragmentation of the forested landscape, will severely affect many population processes, and is expected to have the greatest effect on wildlife species that depend on mature forests, such as the fisher (Carroll *et al.* 1999), pine grosbeak, Hammond's flycatcher, red-backed vole (Raphael 1989), and woodland caribou (Smith *et al.* 2000). The importance of landscape-level structure and composition in dictating wildlife occurrence and abundance has been previously documented (e.g., Pearson 1993; McGarigal and McComb 1995; Drolet *et al.* 1999; Vernier *et al.* 2002).

Many furbearers generally depend on, and are most successful in, continuous, mature forest landscapes. In the Pacific Northwest, marten categorically avoided nonforested habitats and selected mature forest stands containing at least 25% conifers (Poole *et al.* 2004) and complex physical structure near the ground, such as that provided by understorey vegetation, fallen trees, and low overhanging branches (Buskirk and Powell 1994). Similarly, fisher in the Pacific Northwest are closely associated with late seral forests, and prefer structurally complex habitats created by a diversity of tree types, small gaps in the tree canopy, fallen trees, and layers of overhead cover (Allen 1983; Harris *et al.* 1982; Ruggiero *et al.* 1991; Thomas *et al.* 1993; Lyon *et al.* 1994). Lynx are closely associated with the occurrence and distribution of snowshoe hare, which inhabit forested areas with dense conifer thickets (Koehler and Aubry 1994). Lynx are more tolerant of openings than the fisher and marten (Lyon *et al.* 1994), but nonetheless require late seral forests for denning and reproduction. Both fisher and marten are susceptible to forest fragmentation—fisher are not effective at colonizing isolated patches of habitat and marten have low dispersal capabilities (Lyon *et al.* 1994).

Defoliation of beetle-killed trees affects ungulates primarily through the destruction of thermal and security cover. Moose, elk, mule and white-tailed deer, and caribou are designated as species having potential

winter range requirements (Bunnell *et al.* 2004). In cold winters or winters with deep snow, ungulates require the thermal protection and snow interception offered by a closed canopy forest. Ungulate habitat requirements in the summer include thermal cover to reduce heat stress and security cover to escape predation.

The effects of defoliation on wildlife are magnified when the largest trees are selectively attacked by MPB (Safranyik 2004). Large trees are especially valuable as wildlife habitat because of their very deep and complex crowns. These crowns create a diversity of niches for birds and small mammals, and provide a microclimatic gradient from high, exposed radiation environments at the top to buffered environments toward the forest floor (Spies and Franklin 1996). In addition to vertical niche stratification, horizontal stratification is sometimes evident, with different species occupying areas at the edge and at the core of the crown. Large trees also have rough bark that harbours arthropods for bark-gleaners (Adams and Morrison 1993) and provides opportunities for bats and birds (e.g., brown creepers) to nest under the bark. Large trees are also big enough for use by larger species (Oli *et al.* 1997); for example, Spencer (1987) reported that live trees used by martens for resting were primarily large lodgepole pine. Furthermore, these trees are older and tend to have the heart rot conditions that are favourable to many wildlife species.

The effects of defoliation on wildlife will depend on the degree of defoliation. For example, marten did not avoid stands with a history of 10–15% tree mortality caused by the eastern spruce budworm (Payer and Harrison 2000). Winter home ranges usually had less than 30–35% open or closed regenerating stands, but contained as little as 40–50% uncut forest in Quebec (in deciduous and mixed stands; Potvin *et al.* 2000). Marten densities in partially harvested (60% retention of basal area) mixed hardwoods in Maine were equivalent to those in undisturbed forests (Soutiere 1979). Avian species have responded well to residual tree patches in cutblocks—green tree retention has retained bird communities that are characteristically associated with old-growth forests (e.g., Schieck and Hobson 2000; Schieck *et al.* 2000; Tittler *et al.* 2001).

To the extent that wildlife species are not obligate lodgepole pine users (Chan-McLeod and Bunnell 2004), forest vertebrates should be able to derive similar benefits from fir or spruce. However, in heavily infested, pure lodgepole pine stands, where surviving trees are few and where no other conifers exist, wildlife species that depend on tree foliage will likely decline or even

disappear. For example, Rabenold *et al.* (1998) found that canopy- and subcanopy-foraging species declined more than near-ground and trunk-foraging species following a spruce beetle infestation that reduced canopy closure to half its previous level. Similarly, Matsuoka *et al.* (2001) noted that the tree-nesting ruby-crowned kinglet and its major nest predator, the red squirrel, became less abundant after a spruce beetle outbreak. Following a spruce beetle outbreak, wildlife species such as the Townsend's warbler and the golden-crowned kinglet, which depend on closed canopy mature forests, will be most negatively affected (Collins *et al.* 1999).

The defoliation process will likely proceed at variable rates, but foliage usually changes from green to yellow to red within 3 years after beetle attack, and trees begin to lose foliage 2–4 years after death (P. Rakochy, University of Northern British Columbia, pers. comm., 2005). Complete defoliation of the tree, at which point the snag becomes a grey tree, occurs approximately 3–5 years after tree death.

Loss of Living Tree Bark

Living lodgepole pine bark is consumed by mammals such as voles, porcupines, and moose (Hansson and Gref 1987; Niemela and Danell 1988; Hansson 1994). This food source will be eliminated with the death of the tree, as it is the living cambial layer, not the dead outer bark, that provides nourishment as a food source.

Tree bark harbours arthropods that are consumed by birds adapted to foraging on bark (Adams and Morrison 1993). Bark-gleaners include nuthatches, woodpeckers, sapsuckers, and brown creepers (Ehrlich *et al.* 1988). It is unclear what effect tree death will have on the invertebrate population that inhabits the bark, or on the wildlife species that typically forage on these invertebrates. However, lodgepole pine bark is relatively thin and therefore offers few niches for supporting invertebrates, which will likely mitigate any potential negative effects. Furthermore, lodgepole pine bark is likely to remain virtually intact for as long as the dead tree is standing (Lewis and Hartley 2005). Trunk-foraging species, such as the red-breasted nuthatch and brown creeper, were relatively unaffected by a balsam woolly adelgid insect outbreak that reduced canopy closure by half in spruce-fir forests (Rabenold *et al.* 1998).

Modest changes in the bark condition of beetle-killed lodgepole pine that remain upright (Lewis and Hartley 2005) may inhibit the decomposition processes that are advantageous to wildlife habitat values.

Although western long-eared bats have been documented to roost in lodgepole pine trees (Vonhof and Gwilliam 2000), there is no evidence that bats will roost under lodgepole pine bark in either live or dead trees (Vonhof and Barklay 1996; Bunnell *et al.* 2004). In contrast, bark roosts are more common on western white pine, as the decay process generally results in sheets of bark that loosen and create suitable hollows between the bark and sapwood (Vonhof and Barklay 1996).

Cessation of Cone Production

Lodgepole pine seeds are consumed by many songbirds and small mammals, including voles, crossbills, red squirrels, and flying squirrels (Lotan and Perry 1983; Sullivan and Klenner 1993; Ransome and Sullivan 1997; Sullivan and Sullivan 2001; Sullivan and Sullivan 2004; Siepielski and Benkman 2004). Red squirrels, which consume spruce seeds, became less abundant after spruce mortality from a spruce beetle outbreak (Matsuoka *et al.* 2001). The decline in seed-eating wildlife species such as red squirrel will cause a ripple effect, with predators such as marten potentially declining as prey becomes less available.

Proliferation of Standing Dead Trees

Standing dead trees or snags that normally make up 5–10% of the forest (Hunter 1990) are vitally important to many wildlife species. Dead and dying trees provide enhanced opportunities for nesting, roosting, denning, perching, and foraging, and will therefore support more wildlife trees than live trees alone. When treetops or branches break off, the breaks become entry points for fungi, which promote decay in the heartwood. The zones of rotten wood are exploited by woodpeckers, which excavate cavities for breeding (Conner *et al.* 1976; Conner and Locke 1982; Harmon *et al.* 1986). Weak cavity-excavators or secondary cavity-users that cannot excavate their own cavities use vacated woodpecker cavities. When a tree has decayed to the point where it is hollow inside, it then becomes a potential denning site for larger species. Though birds are the most common cavity-user, many species of mammals, including bats, fisher, marten, red squirrel, and northern flying squirrel also use cavities (Bunnell *et al.* 2004). Opportunistic use of tree cavities occurs with some species such as porcupine or black bear (Bunnell *et al.* 2004). In addition to providing suitable nesting and denning sites, dead trees provide habitat for invertebrates that are eaten by wildlife, serve as a food storage for animals, and generate important habitat attributes, such as bark slabs and downed wood.

A tree that dies does not automatically become useful wildlife habitat. Standing dead trees vary in their habitat value depending on their size, decay condition before death, and to a certain extent, species. Decay patterns change after tree death, and tree species have characteristic decay patterns. The ideal decay pattern results in a snag that has a soft interior core, but a hard exterior shell. This pattern provides a protective exterior casing and allows for easy excavation on the inside. When a snag is completely soft, then it is primarily of value as a foraging site for insectivores and as a source of downed wood.

Lodgepole pine snags are generally not preferred. This is either because they are too small to accommodate many of the larger species or because their decay patterns are not typically ideal for cavity excavation. Steeger and Hitchcock (1998) noted that red-breasted nuthatches may avoid nesting in beetle-killed trees because the shallow rooting system of lodgepole pine, coupled with the incidence of root disease, may have uprooted the snags before they had decayed to a softened condition. Lewis and Hartley (2005) concluded that decay of beetle-killed pine was relatively slow while trees were standing, and may proceed more rapidly only after the trees have fallen down. A Williams Lake study that focussed on windthrown trees 15–20 years after beetle attack revealed that these had, on average, 75% bark retention (Waterhouse and Armleder 2004). Waterhouse and Armleder (2004) further noted that most of the fallen trees had broken off at the roots. This observation echoes Bull's (1983) comment that beetle-killed lodgepole pine was susceptible to breakage at the base.

The sudden proliferation of lodgepole pine snags after the current MPB epidemic will therefore not confer the same habitat value as the intermittent creation of snags through tree suppression, disease, or insects in endemic situations. In addition to the limitations imposed by the small size of lodgepole pine snags and non-ideal decay patterns, wildlife species will not efficiently exploit the high density of snags as nest sites because many are territorial and will defend snags within their territory against use by other individuals. Moreover, where the beetle epidemic is severe and living trees are few, habitat limitations will likely be imposed by the lack of resources normally provided by live trees rather than by snag availability. Thus, breeding wildlife may need to increase their territories to satisfy all their habitat requirements. With time and appropriate decay, lodgepole pine snags can become useful

habitat elements; for example, Bull (1983) documented woodpeckers excavating cavities in beetle-killed snags that had been dead 3–8 years. Preliminary study results suggest woodpecker use of beetle-killed wood is higher for trees that had been dead 3–5 years than for those dead for less than 3 years (Chan-McLeod, unpublished data). Extensive debarking of trees, which sometimes characterizes extremely heavy infestations, may also accelerate decay rates (Otvos 1979). Nonetheless, the potential habitat value of beetle-killed trees is seriously compromised by the limitations discussed above.

Fall Down of Dead Trees

Large pieces of wood on the ground, commonly referred to as coarse wood, coarse woody debris, or coarse downed wood, are used by more than 179 forest vertebrates in the Pacific Northwest (Thomas 1979). Vertebrates initially exploit newly created downed wood for perches or cover, but as decomposition progresses, the interior of the wood is used. Loose bark also provides places for hiding or thermal cover. Small mammals will burrow into highly decayed logs; their burrows, in turn, facilitate access by amphibians and reptiles (Harmon *et al.* 1986). Downed wood also benefits wildlife by modulating extreme fluctuations in environmental conditions, and by retaining the moisture that is vitally important for amphibians (Aubry *et al.* 1988; Grover 1998).

Fall down of beetle-killed lodgepole pine is expected to begin 3–5 years after tree death, with 25–50% of the snags down within 10 years (Lewis and Hartley 2005). In the Williams Lake area, Waterhouse and Armleder (2004) determined that the fall rate for dead trees was 1.43% per year over a 5.3 year period, which is equivalent to approximately 7.5% stand attrition by year 5. Bull (1983) noted that more than 90% of beetle-killed lodgepole pine were standing 3 years after death, but only 38% remained after 8 years. Snag persistence was better in Oregon, with almost 75% of trees remaining after 10 years (Harvey 1986), and in Montana, with 63% of snags remaining after 8 years (Lyon 1977).

Soil moisture content is the greatest determinant of how long snags will remain standing, with fall rate highest for snags in wet areas (Lewis and Hartley 2005). Tree size is also important (Bull 1983; Mitchell and Preisler 1998; Nishio 2006), with lodgepole pine snags larger than 25 cm diameter at breast height standing slightly longer than snags of lesser diameter (Bull 1983). To the extent that the soil moisture content may increase in stands with high levels of mortality (presumably because of reduced transpiration), fall rates for such stands will

also be higher than for stands with a low mortality rate (Lewis and Hartley 2005).

Wildlife use of fallen trees may be immediate, as in the case of small mammals that exploit fallen trunks and branches as travel corridors, but is likely to increase after decay has advanced sufficiently to change the wood structure. For example, Harmon *et al.* (1986) noted that the peak use of downed wood as a foraging medium by insectivores does not occur until the middle to late stages of decay. Similarly, downed wood will not satisfy other habitat requirements, such as retaining moisture and modulating the micro-environment, until the wood has softened. Given that coarse wood in the Chilcotin Plateau has a decomposition period of 40–50 years (Hawkes *et al.* 2004), its use in the first decade or two may be primarily as avian perches or as cover for small mammals.

The projected increase in surface fuels (Hawkes *et al.* 2005), plus the increased probability of high intensity stand-replacing crown fires in severely infested areas (Feller 2005), amplify the shift in the forest to younger trees following the beetle's selective attack of older trees. Although the shift to a younger age-class distribution benefits wildlife species that thrive in early seral forests, it is detrimental to those that require mature forests. Stand-replacing fires further reduce wildlife habitat values in mixed stands where non-pine conifers occur in either the overstorey or understorey layers, because such fires favour the establishment of lodgepole pine, which are highly adapted to colonizing disturbed areas. Thus, the stand structural complexity that is created by non-pine conifers and favoured by many wildlife species is eradicated by stand-replacing fires.

Deciduous trees, which are highly beneficial to wildlife, may successfully colonize recent burns, but this scenario is likely limited to some mesic or hygric areas. Deciduous trees are favoured by many cavity-nesting birds as well as mammals that den in trees (Paragi *et al.* 1996) because they are shorter-lived and produce the right kind of decay conditions earlier in the rotation. The rich litter layer encourages the proliferation of invertebrates (Valorvirta 1968; Suominen *et al.* 2003) by providing the necessary moisture conditions, food resources, and the high calcium concentrations required for gastropod shell formation (Karlin 1961; Valorvirta 1968). The high invertebrate populations in turn encourage populations of small mammals and amphibians. Small mammals are also attracted to the unique fungal and lichen communities associated with deciduous trees and the deciduous litter, while amphibians benefit from the moist physical conditions.

Enhanced Understorey Production

Open stands allow more light to reach the forest floor and may result in increased shrub production. Understorey vegetation is critical for many wildlife species, providing nest sites, cover (Althoff *et al.* 1997), and food in the form of berries, foliage, seeds, and associated ectomycorrhizal fungi and insects (Carey and Johnson 1995). The abundance of many small mammals, such as Trowbridge's shrew, Pacific water shrew, shrew mole, white-footed vole, long-tailed vole, and Pacific jumping mouse, is strongly associated with shrub occurrence and volume (McComb 1994). Likewise, the abundance of other shrub-users such as snowshoe hare will increase with increasing shrub cover (Koehler 1990). Increases in wildlife species that prefer open habitats may lead to other changes in the wildlife community. For example, as snowshoe hare populations rise, so will the abundance of predators such as lynx whose populations are highly dependent on the prey base.

The mortality of lodgepole pine after a beetle attack encourages both the development of shrubs and the accelerated growth of spruce and Douglas-fir regeneration in the understorey (Hawkes *et al.* 2004). In mixed conifer stands, beetle outbreaks result in the release of previously shaded survivors which benefit from the improved growing conditions (Hawkes *et al.* 2004); however, the accelerated growth rate of smaller residual trees does not compensate for the loss in tree volume and density (Hawkes *et al.* 2004).

Modest insect attacks have been shown to benefit wildlife species that typically associate with mature forests. For example, marten preferred the dense coniferous shrub layer that resulted from a 15–20 year old spruce budworm epidemic in boreal deciduous and mixed forest stands (Potvin *et al.* 2000). The level of defoliation cannot be excessive, however, as marten usually avoided areas with more than 30–35% open or closed regenerating stands or areas with less than 50–60% mature forests. Understorey-nesting birds also became more abundant in subalpine forests that had high tree mortality from a spruce beetle outbreak

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(Matsuoka *et al.* 2001). Matusoka *et al.* (2001) attributed this population growth to the increased abundance of shrubs as well as to lower predation rates from red squirrel, whose populations decreased after the spruce beetle outbreak.

Factors Governing the Nature of Mountain Pine Beetle Effects and Implications for Forest Management

Several critical factors govern the nature and the magnitude of MPB effects on wildlife and wildlife habitats, including time since tree death, the residual green component, ecosystem type, and landscape-related effects. These factors are summarized here in the context of their implications for forest management.

Time Since Death

The effects of the MPB on wildlife are not static, but are intimately tied to the forest stand dynamics following beetle attack, and hence to time since tree death. This has the following implications for forest management.

- In the very short term (3–5 years), wildlife species that require mature forest cover will be less affected by extensive beetle-kill than by salvage logging, which will immediately revert the forest to an early successional stage.
- As the unsalvaged stand breaks up over time, it becomes increasingly unfavourable to wildlife species that depend on mature forest cover; in certain ecosystems, the rejuvenation of the unsalvaged stand will possibly be slower than that of the salvaged stand.
- In the mid- to long term, unsalvaged stands with high levels of tree mortality will primarily benefit wildlife species that thrive in open or edge habitats, or those that benefit from coarse downed wood.
- To minimize the window when mature forest cover may be scarce or non-existent in extensively defoliated landscapes, forest managers should attempt to balance the landscape mosaic of unsalvaged beetle-killed stands, with their declining habitat value for wildlife that prefer mature forests, and salvaged stands, with their slowly increasing habitat value for such species.
- Forest managers should also strive to balance the landscape mosaic to accommodate habitats for wildlife species that prefer mature forests and species that prefer open environments (which will likely benefit from both salvaged and unsalvaged situations).

Residual Green Component

The effects of the MPB infestation on wildlife will depend on the severity of defoliation and the type and amount of live vegetation remaining after the attack. The residual green component is governed by the mortality rate of lodgepole pine after beetle attack, the occurrence of non-pine trees that are not susceptible to beetle-caused mortality, and the possible occurrence of an understory of regenerating, shade-tolerant tree species as well as shrubs and herbs. Forest managers should limit salvage operations where habitat values are highest following the beetle infestation. In particular, high habitat values after beetle attack will occur in:

- Uneven-aged forest stands: Surviving younger trees that escaped beetle attack will experience accelerated growth following the opening of the canopy, and will counter the loss of trees from the beetle-kill. Advance regeneration in the understory will also reduce the time required to regenerate mature tree cover. The structural complexity of uneven-aged stands also provides high habitat values to wildlife.
- Stands with mature residual, live non-pine trees in the co-dominant or dominant layer, or pine that escaped the infestation: The interspersed of open and closed forested habitats mitigates the detrimental effects of open areas on wildlife that depend on mature forest. Many wildlife species that depend on mature forest or continuous forest cover are able to survive in partially defoliated areas, although population size may decline. Furthermore, the complex stand structure and high habitat values provided by the non-pine components will also continue to support these species. The interspersed of open and closed forested habitats, which provides a varied mosaic of stand types, also helps to maintain landscape connectivity for dispersing or migrating wildlife and to support an increased diversity of wildlife.
- Stands with a well-established shrub layer: Although many wildlife species do not require tree cover, the

majority of these species do require shrub cover. Shrub production is enhanced when the canopy is opened up, unless soil moisture or environmental conditions are limiting. The existing and accelerated shrub growth benefits species that prefer open habitat, as well as those species that prefer edge habitats (e.g., deer, which have dual requirements for both open and closed habitats).

Ecosystem Type

The environmental conditions that characterize each ecosystem type will mediate the processes by which the pine beetle affect wildlife and wildlife habitat. Salvage logging decisions should consider the following factors regarding ecosystem type.

- The habitat values of forest stands will vary depending on ecosystem type even before an MPB infestation. Ecosystems that supported few wildlife species before an infestation will likely retain nominal habitat values after the attack. Forest managers should preserve stands that had high biodiversity values before the attack as many important habitat attributes will likely be unaffected by pine mortality. Important habitat attributes include stand structural complexity, riparian areas, mixtures of tree species, deciduous trees, large veterans, and large snags. Ecosystems that had low wildlife habitat values before a beetle infestation will be relatively unaffected by the potentially negative effects of the beetle epidemic.
- Ecosystems in which environmental conditions (e.g., soil moisture) seriously limit plant growth may not experience the enhanced shrub production or accelerated growth of released trees following the opening of the pine canopy. For example, open pine stands with a well-established grass cover will probably experience nominal accelerated growth of understory regeneration, if the shrub layer was previously sparse or non-existent. Forest regeneration may be inhibited in such situations because the accelerated growth of released trees is more important than seedling establishment when a well-established grass layer has not been disturbed.
- The benefits of snags created by the beetle attack are limited in ecosystems with high soil moisture or high wind exposure: these snags may never attain a suitable degree of decay for cavity-nesters before falling over.

The effects of the MPB infestation on wildlife will depend on the severity of defoliation and the type and amount of live vegetation remaining after the attack.

Landscape Effects

The surrounding landscape characteristics will shape the response of wildlife to unharvested, beetle-attacked stands. Forest managers should recognize that:

- The effects of insect defoliation will be minimal if the infestation is localized and the surrounding landscape offers extensive mature forest cover. Salvage logging is unnecessary for wildlife conservation in such situations and is possibly harmful.
- The potentially negative effects of insect defoliation on wildlife will be magnified in an extensive landscape of beetle attack. Rapid re-establishment of mature forest cover, in balance with retention of structural elements, may be of paramount importance if a landscape is extensively affected by the infestation—insect defoliation and salvage logging both eradicate the mature forests required by many wildlife species.

Conclusions

The effects of the MPB infestation on wildlife and wildlife habitats will change with the forest stand dynamics after beetle attack. In the absence of salvage logging, wildlife will experience relatively minor detrimental effects over the short term, but the beneficial effects will be conspicuous. For example, a pronounced spike in numbers of woodpeckers and other insectivorous species will occur, but the detrimental effects of extensive tree mortality on wildlife values will not have fully manifested because the trees remain virtually intact. For wildlife species that depend on the forest for cover, the negative effects of the MPB infestation will become more apparent when the dead trees drop their foliage. When this happens, a ripple effect may occur in the food chain, as predators who prey on these species also experience declines. As successive waves of beetle attacks pass through a stand, suitable brood trees become unavailable, and the temporary spike in the food supply for woodpeckers and for insectivores that feed on the adult beetle is concluded. After 8–10 years, as the stand opens up significantly from the fall-down of snags, beneficial effects accrue to wildlife species that thrive in open conditions, and to a lesser extent, to wildlife species that have requirements for mature forest attributes, such as adequately decayed snags and downed wood. At each stage of a stand's trajectory after beetle attack, the effects on wildlife will critically depend on the severity of attack, the type and amount of remaining live vegetation, the ecosystem type, and the surrounding landscape. Forest managers should consider all these factors when evaluating the ecological legacy of beetle-attacked stands.

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ARTICLE RECEIVED: February 3, 2006

ARTICLE ACCEPTED: September 11, 2006

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Test Your Knowledge . . .

A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest 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. The effects of the mountain pine beetle on wildlife will depend on:
 - A) Time since beetle attack
 - B) Level of defoliation and the amount and type of residual live vegetation
 - C) Surrounding landscape characteristics, including the forest cover composition and the extent of the beetle attack
 - D) All of the above

2. The effects of the beetle-killed stands on wildlife species that require mature forest cover are expected to be most severe beginning:
 - A) Within 6–12 months after beetle attack
 - B) 8–15 years after beetle attack
 - C) 80–100 years after beetle attack

3. The mountain pine beetle infestation will always have negative effects on wildlife and wildlife habitats.
 - A) True
 - B) False

ANSWERS

1. D 2. B 3. B