

The response of mammals to forest fire and timber harvest in the North American boreal forest

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ABSTRACT

1. This paper reviews and compares the effects of forest fire and timber harvest on mammalian abundance and diversity, throughout successional time in the boreal forest of North America.

2. Temporal trends in mammal abundance and diversity are generally similar for both harvested and burned stands, with some differences occurring in the initiation stage (0–10 years post disturbance).

3. Small mammals and ungulates are most abundant immediately post disturbance, and decrease as stands age. Lynxes and hares utilize mid-successional stands, but are rare in young and old stands. Bats, arboreal sciurids and mustelids increase in abundance with stand age, and are most abundant in old growth.

4. Substantial gaps in the data exist for carnivores; the response of these species to fire and harvest requires research, as predator–prey interactions can affect mammal community structure in both early and late successional stages.

5. The lack of explicit treatment of in-stand forest structure post disturbance, in the reviewed literature made comparisons difficult. Where forest structure was considered, the presence of downed woody material, live residual trees and standing dead wood were shown to facilitate convergence of mammal communities to a pre-disturbance state for both disturbance types.

6. Mammalian assemblages differed considerably between successional stages, emphasizing the importance of maintaining stands of each successional stage on the landscape when implementing forest management strategies.

Keywords: conservation, fire, forest mammals, forest management, harvesting

INTRODUCTION

Innovations in forest management theory have led to the development of the natural disturbance emulation paradigm, wherein timber harvest patterns are designed to mimic natural disturbance such as forest fires. The rationale behind the natural disturbance model is that boreal forest biota are adapted to fire; by logical extension, a timber harvest regime that mimics fire, and is somewhat compensatory, would result in forest disturbance within the range of biotic tolerance.

Many single-species studies have been conducted to test the comparative responses of a boreal mammal to forest fire or timber harvest within one or two successional stages, but an integration of these studies, and an analysis of the trends, has been lacking. The goal of

this paper is to assemble and review existing studies; to detect trends in the response of mammalian species to forest fire and timber harvest over successional time; to provide some extrapolation from other ecotypes; and to identify gaps in our knowledge of responses to stand-level disturbance.

We track changes in mammal diversity and abundance, in both burn-origin stands and harvest-origin stands as they proceed through the stages of forest succession: the initiation stage (0–10 years post disturbance), establishment stage (11–25 years), aggradation stage (26–75 years) and mature/old growth stage (76–125+ years). Descriptions of these successional stages in the North American boreal forest can be found in Lee (2002). We group studies according to the disturbance type and age of the stands analysed; where possible, we compare mammals' response to timber harvest and fire within each successional stage. We focus on the North American boreal forest, but also include some information from boreal Fennoscandia, and non-boreal regions where applicable.

More than 25 boreal mammal species are included in this review. Many of those species examined respond similarly to forest disturbance throughout successional time, making a species-by-species account cumbersome. In addition, data for many species, successional stages and disturbance types do not exist. For these reasons, we group some mammal species together based on taxonomic classifications. In some cases, such as with Order Rodentia (here including squirrels and mice), taxonomic groups have been split. These species groups instead follow shared life histories, because of similarities between species group members in their response to forest disturbance. Where data are lacking for a species group, this has been noted. The data gaps revealed by this review are as important as the data trends; these gaps indicate where further study is required, and highlight where known information can help guide forest and mammalian management efforts. A summary of mammals' response to forest disturbance through successional time is presented in Table 1.

When comparing between studies, it must be recognized that burned (or harvested) stands are not uniform. Remnants of unburned trees and vegetation are left behind, from which species migrate and repopulate burns (Hooven, 1969; Buech *et al.*, 1977). The variability in the amount and distribution of these fire skips – and their postharvesting equivalent, live residual trees – can significantly influence the mammalian assemblage occurring in a stand after disturbance. If retained in sufficient quantities, residuals may provide habitat for old-growth-associated plant (e.g. lichen, Sillett & Goslin, 1999) and mammal species in earlier seral stages than would occur if residuals were absent. Retention of residuals and standing dead trees, or snags, is particularly important in short rotation stands, where old-growth attributes may not develop (Harris & Maser, 1984). Therefore, within each species group, we also review available literature on the importance of fire skips and live residual trees to the maintenance of this species group post disturbance.

SMALL MAMMALS: RODENTIA AND INSECTIVORA

Initiation stage

Forest fire

The response of the small mammal community – including deer mice *Peromyscus maniculatus*, southern red-backed voles *Clethrionomys gapperi*, meadow voles *Microtus pennsylvanicus*, meadow jumping mice *Zapus hudsonius*, woodland jumping mice *Napaeozapus insignis*, least chipmunks *Tamias minimus* and shrews *Microsorex*, *Blarina* and *Sorex* spp. – to forest fire is variable. Where fire is a recurring disturbance on the landscape, changes in small mammal communities are manifested as shifts in relative abundance, rather than as a sequential replacement of species (Fox, 1990). Burn severity, site characteristics, successional stage and

Table 1. A summary of changes in mammal abundance by species group throughout successional time. Descriptions include the response to both harvested and burned stands

Species group	Initiation stage 0–10 years Absence of trees and canopy cover; DWM abundant in burns but variable in clearcuts	Establishment stage 11–25 years Shrubby and herbaceous vegetation cover increase, grasses decrease	Aggradation stage 26–75 years Tree density and canopy cover increase, shrub and herbaceous cover decrease	Old growth stage 76–125+ years Heterogeneous canopy and stand structure, developed understorey, large trees and snags, DWM, canopy gaps
Rodents & insectivores	Variable; generally positive response with shifts in relative abundance of different species (i.e. red-backed voles to meadow voles and deer mice); shrew abundance stable or increasing (limited data); recolonization rates increase with amount of DWM	Variable; granivores decrease; red-backed voles begin to dominate small mammal community; shrews may become less abundant in clearcuts	Deer mice most abundant small mammal species, although abundance of all voles and mice is lower than in other stages; variable response by shrews	High species richness; red-backed voles and shrews most abundant at this stage; deer mice less abundant (dominance shift reversal from initiation stage)
Arboreal sciurids	Absent or in very low abundance because of lack of escape cover, food and nesting sites	Low abundance	Low abundance	Red and flying squirrels abundant because of widely available escape cover, food and nesting sites
Bats	Some foraging activity; lack of roost sites	Low activity	Low activity	Excellent roost sites; foraging activity varies by species and amount of canopy breakup
Lagomorphs	Absent or low abundance	High abundance because of well developed understorey for browse and escape cover	Abundance decreases as understorey decreases	Low abundance because of insufficient escape cover
Ungulates	Low caribou abundance because of lack of lichen, especially in burns; other ungulates will use sites for foraging, with moose being most abundant, particularly in clearcuts	Low caribou abundance; high moose abundance, increasing abundance of other ungulates because of increasing cover	Increasing caribou use as lichen increases; moose abundance decreasing (higher in clearcuts than in burns)	Preferred stage for caribou; moose abundance generally low; suitable cover for other ungulates
Mustelids	Generally low use of burns; martens may use burns and clearcuts as marginal habitat; small mustelids forage in slash piles	Martens may use burns and species clearcuts, but these remain poor-quality habitat; no data on other species	Low marten abundance because of poor habitat for prey species (i.e. meadow voles); no data on other species	High marten abundance; fisher recognized as old-growth species although data generally lacking
Canids, Felids & Ursids	Poor data; bears will use these stands for foraging; canids will likely use both burned and logged stands	Variable; high lynx abundance because of snowshoe hares; canids and black bears present but abundance is unknown	Variable; lynx abundance follows hare abundance; grizzly bears and wolves present but abundance is unknown	Minimal data; foxes and lynxes in low abundance

surrounding habitat also influence small mammal distribution and abundance in burns (Black & Hooven, 1974). Typically, small mammal abundance increases with stand age after fire, in a manner that corresponds with species-specific habitat associations (Simon *et al.*, 1998). Granivores dominate early successional sites; foliovores follow when grasses and sedges appear; and omnivores appear on tree-dominated sites (Fox, 1990).

In the initial postfire period, the small mammal community is dominated by deer mice; they commonly colonize areas following disturbance (Hooven, 1969), and can sometimes survive low-intensity fires. As generalist omnivores (Walters, 1991) deer mice are able to find food in burns, particularly in conifer stands where seeds are often abundant. Immediately following wildfire, deer mice were more abundant in burned than unburned jack pine stands, while the opposite trend occurred in mixedwood stands (Buech *et al.*, 1977). However, only juveniles were present, suggesting that recent burns may be dispersal sinks. In Minnesota mixedwood stands, deer mice dominated the small mammal community for the first 7 years post fire, but decreased in the following 6 years.

Southern red-backed voles are often considered old-growth specialists, because of their association with dense cover, mesic microclimates, and downed woody material (DWM; Morris, 1969; Miller & Getz, 1977; West, Ford & Zasada, 1980; Yahner, 1986; Wywiałowski & Smith, 1988; Nordyke & Buskirk, 1991). Despite these habitat associations, southern red-backed voles have occurred in young burns in boreal Alberta (Corkum, 1999), and have repopulated burns within 3 years following wildfire (Krefting & Ahlgren, 1974; Simon *et al.*, 1998).

As grasses typically dominate the plant community after fire, grassland species such as meadow voles and jumping mice colonize burns (Krefting & Ahlgren, 1974). Meadow voles, in particular, are associated with grassy cover (Adler & Wilson, 1989), and have been found in 3-year-old black spruce burns (Simon *et al.*, 1998).

As insectivores, shrews are less directly dependent on the plant community compared to herbivorous small mammals (Kirkland, 1977). Thus, changes in shrew populations resulting from fire and timber harvest may not be as dramatic as for other small mammal species (Gunther, Horn & Babb, 1983; Probst & Rakstad, 1987). However, most shrew species, including the masked shrew *Sorex cinereus*, require hydric and mesic microclimates, and are associated with litter and shrub cover (Getz, 1961; Wrigley, Dubois & Copland, 1979; MacCracken, Uresk & Hansen, 1985). Consequently, shrews may not be present after intense fires that consume the litter layer (Black & Hooven, 1974). Masked shrews have occurred post fire, but at lower abundance than in prefire stands (Buech *et al.*, 1977). Conversely, Krefting & Ahlgren (1974) did not detect any changes to shrew populations following wildfire in mixedwood stands.

Least chipmunks may be common in burns when a variety of seeds are available (Krefting & Ahlgren, 1974), but typically forage around edges to avoid predation (Nupp & Swihart, 1998) and remain in close proximity to burrows (Bowers, 1995), hence are not expected to be abundant.

Timber harvest

Within the first 10 years following clearcutting, considerable changes occur to the small mammal community (Martell & Radvanyi, 1977; Probst & Rakstad, 1987; Steventon, MacKenzie & Mahon, 1998). Vegetation, in concert with invertebrates found in woody debris and leaf litter, provide food for several species, although fungi are depleted following harvest (Bradbury, Danielson & Visser, 1998). Clough (1987) found that cut and burned (1–4 years old) sites had high diversity of small mammals, but low relative abundance. However, in newly

clearcut mixedwood stands, relative abundance of *P. maniculatus*, *C. gapperi* and *Blarina brevicauda* was not significantly different from adjacent uncut stands (Clough, 1987). Parker (1989) noted higher densities of small mammals in young clearcuts and plantations than in 15- to 17-year-old plantations. Kirkland (1990) reviewed 21 studies investigating harvesting practices on small mammals, and concluded that overall, small mammals demonstrated a positive response to recent clearcuts even though considerable site variation existed.

Deer mice are abundant in recent clearcut coniferous (Gashwiler, 1970; Hooven & Black, 1976; Sullivan, 1979; Ramirez & Hornocker, 1981; Gunther *et al.*, 1983; Walters, 1991; Steventon *et al.*, 1998; Sullivan, Lautenschlager & Wagner, 1999), aspen (Probst & Rakstad, 1987) and mixedwood stands (Moses & Boutin, 2001). Deer mice forage on abundant seeds and insects in clearcuts (Tevis, 1956; Hooven & Black, 1976; Gunther *et al.*, 1983); increased cover has been associated with higher densities and higher overwinter survivorship of deer mice (Van Horne, 1982). In contrast, Miller & Getz (1977) found that deer mice were more abundant in habitat with less herbaceous cover. In his review, Kirkland (1990) noted that in general, deer mice showed a positive initial response to clearcutting in coniferous stands, but tended to decline in deciduous stands, where there was less postharvest seedfall. Peak densities typically occur 2–5 years post harvest (Martell & Radvanyi, 1977; Ramirez & Hornocker, 1981; Martell, 1985a), though in aspen stands, densities were higher in 1-year-old cutblocks than in older cutblocks (Probst & Rakstad, 1987). Early recruitment in clearcuts suggests that they may act as sinks for subordinate and juvenile deer mice (Sullivan, 1979; Martell, 1985a), thus representing suboptimal habitat. In contrast, Moses & Boutin (2001) found no evidence that reproductive and survival rates of deer mice were affected by logging.

Southern red-backed voles occur in clearcuts, but disparity between stands emphasizes the significance of site-specific differences and their effects on small mammal communities (Martell, 1985a). Several studies have documented low abundance of red-backed voles in young coniferous (Tevis, 1956; Gashwiler, 1970; Sims & Buckner, 1973; Hooven & Black, 1976; Martell & Radvanyi, 1977; West *et al.*, 1980; Scrivner & Smith, 1984; Martell, 1985a,b; Steventon *et al.*, 1998; Sullivan *et al.*, 1999), aspen (Probst & Rakstad, 1987) and mixedwood clearcuts (Moses & Boutin, 2001). In contrast, others have found that red-backed voles were only slightly reduced (Hayward, Henry & Ruggiero, 1999) or were abundant in coniferous (Gunther *et al.*, 1983; Monthey & Soutiere, 1985; Walters, 1991) and hardwood clearcuts (Kirkland, 1977). Kirkland (1990) concluded that most studies recorded an initial positive response by voles to clearcutting, and that *C. gapperi* was the species responsible for the overall increased abundance of microtines in clearcuts.

However, this high initial abundance of red-backed voles may not persist. In black spruce cuts, red-backed voles initially dominated small mammal communities, but declined by the end of the second or third summer following harvest, by which time deer mice were dominant (Martell & Radvanyi, 1977; Martell, 1985a). Similarly, Monthey & Soutiere (1985) found that red-backed vole abundance was higher in 1- to 3-year-old clearcuts than in 4- to 8-year-old clearcuts. Ground cover occurring after 3–4 years may be necessary to create suitable levels of soil and litter moisture for red-backed voles, possibly by accumulating dew (Hooven, 1969). Kirkland (1990) noted that herbaceous plants in clearcuts tend to accumulate more dew cover than the same plants in adjacent forest, thereby creating suitable habitat for some forest-associated species.

Meadow voles are common in young clearcuts (Martell & Radvanyi, 1977; Gunther *et al.*, 1983; Probst & Rakstad, 1987; Steventon *et al.*, 1998; Moses & Boutin, 2001). Kirkland's (1990) review noted that meadow voles were typically present in clearcuts in moist regions.

Similarly, meadow jumping mice also respond favourably to clearcutting (Kirkland, 1990). They have been recorded in grassy areas of cutblocks (Probst & Rakstad, 1987; Sekgororoane & Dilworth, 1995), exhibiting higher abundance in deciduous cutblocks than in coniferous cutblocks (Kirkland, 1977). Long-tailed vole *Microtus longicaudus* abundance was also significantly greater in clearcuts than in forested stands, in British Columbia (Sullivan *et al.*, 1999). In Scandinavia, abundance of the bank vole *Clethrionomys glareolus* was highest in recent cuts compared to older stands. However, there was high turnover and low survival rates in young stands, indicating young stands were suboptimal habitat (Ecke, Löfgren & Sörilin, 2002).

Chipmunks generally showed a positive response to clearcutting (Kirkland, 1990). Least chipmunks have been found in clearcuts where they were associated with cutblock edges (Martell & Radvanyi, 1977; Probst & Rakstad, 1987). Northwestern chipmunk *Tamias amoenus* abundance was greater in clearcut sites than forested sites in British Columbia.

Shrews tend to be more common in recently harvested sites compared to recently burned sites, because of a comparative lack of litter, vegetative cover and DWM within burns. In both, invertebrate prey associated with the breakdown of woody debris likely provide shrew forage. Parker (1989) found that insectivores (*Sorex* spp.) were the primary recolonizers of conifer stands post harvest, and that their numbers declined with stand age. Kirkland (1990) concluded that shrews generally exhibited a positive response to clearcutting in conifer (Sekgororoane & Dilworth, 1995; Steventon *et al.*, 1998), hardwood (Kirkland, 1977) and aspen (Probst & Rakstad, 1987) stands. In addition to food availability, shrews may take advantage of a moist microclimate created by heavy dew and shading (Wrigley *et al.*, 1979; MacCracken *et al.*, 1985) in regenerating cutblocks.

Establishment stage

Forest fire

As burns regenerate, increasing vegetative cover and decreasing grassy cover leads to changes in small mammal species dominance. In 20- to 30-year-old boreal mixedwood stands, red-backed voles and masked shrews were common, but were less abundant than in old stands (Roy, Stelfox & Nolan, 1995). Grassland species are food-limited during this successional stage; not surprisingly, meadow voles were uncommon, and jumping mice absent, in mixedwood stands (Roy *et al.*, 1995). Similarly, in 20-year-old black spruce stands, red-backed voles and masked shrews were common, and meadow voles were absent (Simon *et al.*, 1998). Deer mice, which are positively associated with large DWM and negatively associated with grass cover, willow and small tree density in mixedwoods, were found throughout this successional stage, but at lower abundance relative to mature stands (Roy *et al.*, 1995). Arctic shrews (*Sorex arcticus*); dusky shrews (*S. monticolus*) and pygmy shrews (*S. hoyi*) occurred at this stage in mixedwoods (Roy *et al.*, 1995).

Timber harvest

Red-backed voles, deer mice, masked shrews and chipmunks have been found in clearcuts at this stage that exhibit dense shrub cover (Parker, 1989; Walters, 1991). Red-backed voles tended to be at higher densities during the 11- to 25-year-old successional stage compared to more recent clearcuts (Monthey & Soutière, 1985, Probst & Rakstad, 1987). Conversely, densities of deer mice (Ramirez & Hornocker, 1981; Probst & Rakstad, 1987), shrews (Kirkland, 1977) and other small mammals (Parker, 1989) have been found at lower densities at this stage compared to younger clearcuts or plantations. Kirkland (1977) detected a decrease in abundance of granivorous small mammals in deciduous cutblocks, but not in coniferous

cutblocks, of this age. Populations of meadow voles (M'Closkey, 1975) decrease throughout this successional stage.

Aggradation stage

Forest fire

During this successional stage, tree density and canopy cover increase, and consequently shrub and herbaceous cover decrease. Roy *et al.* (1995) concluded that 50- to 65-year-old mature stands had lower species richness than either young or old stands. There is, however, a great deal of variability among studies.

Roy *et al.* (1995) found that deer mice had a positive association with 50- to 65-year-old mature stands, and were the most abundant small mammals at this stage. Deer mouse abundance was negatively related to canopy heterogeneity. Meadow voles were found in aggradation stage stands, but at lower abundance relative to early successional stages, and to red-backed vole and deer mice abundance (Roy *et al.*, 1995). Meadow jumping mice were also associated with aggradation stage stands (Roy *et al.*, 1995).

Red-backed voles were common at this stage (Roy *et al.*, 1995), but were less abundant relative to young and old stands (Roy *et al.*, 1995). Moreover, red-backed vole abundance was greater, and body condition better, in spruce/fir stands at the end of this successional stage compared to younger stands (Nordyke & Buskirk, 1991). Older stands exhibited old-growth characteristics, including large, old trees, a multilayered canopy, large amounts of DWM and mesic microhabitats. Vole abundance was positively correlated with understorey cover and, to a lesser extent, decay stage of logs (Nordyke & Buskirk, 1991).

Like red-backed voles, masked shrews were least abundant in 50- to 65-year-old mixedwood stands compared to young and old stands (Roy *et al.*, 1995). Wrigley *et al.* (1979) observed that masked shrews were uncommon in stands with dense canopy cover.

Timber harvest

Scrivner & Smith (1984) found that deer mice and red-backed voles were common throughout this stage, the latter being more abundant in mid- to late-successional stands than in young clearcuts. Jumping mice were also more abundant in mid-successional stages than in early- or late-successional stages. In Newfoundland, Thompson & Curran (1995) found that meadow voles were rare in 40 to 60-year-old stands, while masked shrews (*S. cinereus*) were ubiquitous. Chipmunks were also found in mid-successional sites, where the closed canopy provided protection from predation (Bowers, 1995).

Old growth stage

A heterogeneous canopy and stand structure, well developed understorey layer, large trees and snags, DWM and canopy gaps are all characteristics of old stands. These attributes constitute suitable habitat for many small mammal species.

In boreal Alberta, old mixedwood stands (120+ years old) supported a greater mammalian species richness compared to young and mature stands (Roy *et al.*, 1995). Canopy gaps improved habitat for several species; gaps supported increased shrub cover and provided protection, moisture and diverse food sources (Roy *et al.*, 1995). In contrast, in British Columbia, small mammal species richness and diversity was low in uncut stands (Sullivan & Sullivan, 2001), when compared with high deer mouse and meadow vole abundance in newly harvested stands.

Deer mice may be common in old-growth stands (e.g. Scrivner & Smith, 1984), as snags provide denning and nesting sites for deer mice (Wolff & Hurlbutt, 1982). However, in old

mixedwood stands, they were considerably less abundant than in mature stands (Roy *et al.*, 1995). Red-backed voles were significantly more abundant in old stands than in young or mature stands (Roy *et al.*, 1995; Sullivan, Sullivan & Lindgren, 2000). Red-backed vole abundance was positively associated with canopy heterogeneity, DWM and density of large snags and shrub/saplings (Roy *et al.*, 1995). Nordyke & Buskirk (1991) noted that red-backed vole abundance was greater in old-growth conifer stands with canopy gaps than in closed-canopy mature stands. Walters (1991) also documented high vole abundance in old-growth conifer stands. Similarly, Simon *et al.* (1998) found that 110-, 130-, and 150-year-old black spruce stands were dominated by red-backed voles, where they were positively associated with tree height, broad-leaved shrub cover and large woody debris, and were negatively associated with dry sites.

Masked shrews were also abundant in old-growth conifer (Walters, 1991), mixedwood (Roy *et al.*, 1995), black spruce (Simon *et al.*, 1998) and balsam fir (Thompson & Curran, 1995) stands. Shrews were more abundant in old mixedwood stands than in young or mature stands; they were positively associated with canopy heterogeneity and density of large snags and shrub/saplings (Roy *et al.*, 1995). In old-growth black spruce stands, masked shrews were positively associated with shrub cover (Simon *et al.*, 1998).

Live residual trees

Live residual trees have been shown to facilitate the maintenance of small mammal population post disturbance (Von Trebra, Lavender & Sullivan, 1998). This occurs mainly through a long-term infusion of DWM into the burn (or cutblock); DWM is an integral habitat component for many small mammal species (Tevis, 1956; Gunderson, 1959; Wolff & Hurlbutt, 1982; Monthey & Soutière, 1985; Wywiałowski & Smith, 1988; Nordyke & Buskirk, 1991; Planz & Kirkland, 1992; Tallmon & Mills, 1994). DWM provides cover, moist microclimates, travel paths, burrow sites and a substrate for food such as fungi, lichen, plants and invertebrates (Gashwiler, 1959; Gunther *et al.*, 1983; Maser, Maser & Trappe, 1985, Carey & Johnson, 1995).

ARBOREAL MAMMALS: SCIURIDS

Initiation stage

Forest fire

The red squirrel *Tamiasciurus hudsonicus* is a conifer seed specialist (Kemp & Keith, 1970; Rusch & Reeder, 1978). Fire destroys seed sources and den sites; although the squirrels have been found in <10-year-old burned mixedwood stands, red squirrels likely forage opportunistically for supplementary foods in these areas, rather than colonize them as fully utilized home ranges (Fisher, 1999). Crête *et al.* (1995) found red squirrel abundance increased with stand age post fire. Although wildfires typically leave standing wood, dead trees provide little protective cover for red squirrels, or for northern flying squirrels *Glaucomys sabrinus*. Key habitat components for flying squirrels are absent from burn sites. These components include large live and dead trees for dens (Mowrey & Zasada, 1984; Rosenberg & Anthony, 1992; Witt, 1992; Carey, 1995) and fungal and lichen food sources (Rosenberg & Anthony, 1992, Maser *et al.*, 1985, 1986; Waters & Zabel, 1995).

Timber harvest

Both red and northern flying squirrels are found infrequently in recently harvested sites. Thompson *et al.* (1989) found that red squirrel tracks were less abundant in young clearcuts than in old cuts and uncut stands. Red squirrels did occur in aspen cutblocks in Alberta

(Fisher, 1999), but cutblocks were occasional summer foraging grounds, rather than a core part of a defended territory. Though conifer specialists, red squirrels also feed on seasonally produced berries and fungi that are found in young regenerating cutblocks with flowering shrub growth. The juxtaposition of spruce stands, aspen stands and cutblocks was a significant positive predictor of squirrel presence in the summer (Fisher, Boutin & Hannon, in press), indicating that the arrangement of cutblocks on the landscape can influence the distribution of this arboreal sciurid.

Northern flying squirrels would be expected to be largely absent from cutblocks without live residuals because of a lack of large old trees for den sites and cover (see Carey *et al.*, 1999). Kirkland (1990) found that the response of squirrels to clearcutting was variable, although in general, abundances of tree-dwelling species such as red squirrels and northern flying squirrels were reduced in clearcuts.

Establishment stage

Forest fire

At this stage, food and nest sites remain limited for northern flying squirrels and red squirrels. During winter, red squirrels were associated with 20- to 30-year-old mixedwood stands, but were less common in summer (Roy *et al.*, 1995). Yahner (1987) observed that red squirrel feeding sites were associated with high densities of understorey trees, low densities of shrubs, and were in close proximity to overstorey conifers-bearing cones; such conifers are largely absent in burns of this age. Twenty-year-old lodgepole pine and 110-year-old mixed conifer stands had similar red squirrel densities throughout the year, although young stands had low survival, low proportion of breeding females and high fall recruitment, suggesting that 20-year-old stands acted as dispersal sinks (Sullivan & Moses, 1986). Northern flying squirrels were uncommon in 20- to 30-year-old mixedwood stands in Alberta (Roy *et al.*, 1995); deciduous saplings provide minimal protection for flying squirrels (Mowrey & Zasada, 1984).

Timber harvest

Red squirrel abundance is lower in clearcuts of this age class than in uncut stands, though not significantly different from regenerating clearcuts of other age classes (Thompson *et al.*, 1989).

Aggradation stage

In 50- to 65-year-old burn-origin mixedwood stands, red squirrels were found in relatively low abundance and were negatively associated with the density of small trees (Roy *et al.*, 1995). Ransome & Sullivan (1997) suggested that managed second-growth coniferous stands during this stage are suboptimal habitat for squirrels because of lack of food. Thompson *et al.* (1989) found that red squirrel tracks were less abundant in managed stands of 20+ to 30+ years old than in uncut sites.

Old growth stage

Red squirrels were more abundant in old stands than in mature or young stands, with a strong association for old stands in summer, and a moderate association for young and old stands in winter (Kemp & Keith, 1970; Rusch & Reeder, 1978; Roy *et al.*, 1995). Specifically, squirrels were positively correlated with canopy heterogeneity, sapling density and large trees (Roy *et al.*, 1995). In Ontario, red squirrel tracks were generally more abundant in old uncut stands than in regenerating stands (Thompson *et al.*, 1989). In Alberta's southern boreal forest, red squirrels were most abundant in old/mature mixed spruce stands, followed by jack pine, and

then aspen stands (Rusch & Reeder, 1978). Red squirrels exhibit a preference for old/mature cone-producing stands (Kemp & Keith, 1970), wherein they preferentially nest in large-diameter white spruce trees (Fancy, 1980).

Northern flying squirrels are typically associated with older stands. Flying squirrels were more abundant in old stands than mature or young stands, and are known to commonly inhabit old-growth stands where food (Maser *et al.*, 1985, 1986; Waters & Zabel, 1995) and nest sites are abundant (Mowrey & Zasada, 1984; Rosenberg & Anthony, 1992; Witt, 1992; Carey, 1995; Carey *et al.*, 1997). In California fir stands, flying squirrel densities were greater in 200-year-old stands than in 75- to 95-year-old stands (Waters & Zabel, 1995), although abundance levels similar to those in old-growth have been documented in mature stands where old-growth remnants persist (Rosenberg & Anthony, 1992). Flying squirrels in old mixedwoods were positively associated with white spruce, shrub and sapling densities (McDonald, 1995), as well as intermediate decay stages of DWM, which support fungi and lichen (Roy *et al.*, 1995). In addition, canopy gaps in old forests provided protective shrub cover for flying squirrels foraging on the ground (McDonald, 1995).

Live residual trees

Live residual trees provide long-term infusion of DWM into a stand, which in turn provides cover, travel paths, burrow sites and a substrate for arboreal sciurid food such as fungi and lichen (Gashwiler, 1959; Gunther *et al.*, 1983; Maser *et al.*, 1985; Carey & Johnson, 1995). Some fungal species that are critical dietary components of flying squirrels (Maser *et al.*, 1985, 1986; Waters & Zabel, 1995), are found exclusively on DWM (Carey *et al.*, 1999). Retention of live residual trees also facilitates the maintenance of lichen within a stand, and fosters lichen recolonization of disturbed areas (Sillett & Goslin, 1999); lichen is key food source for flying squirrels (McKeever, 1960; Hayward & Rosentreter, 1994). In addition to DWM, mature residual conifer trees provide conifer seed, important overwintering food sources for red squirrels (Rusch & Reeder, 1978).

BATS

Initiation stage

Forest fire

Habitat use by boreal bats, including *Myotis lucifucus*, *M. septentrionalis*, *M. evotis*, *M. volans*, *Eptesicus fuscus*, *Lasionycteris noctivagans* and *Lasiurus cinereus*, immediately post fire has not been studied. Bat activity levels within burns is expected to be variable, depending on the density of trees left standing; bats tend to avoid foraging in 'cluttered' environments (stands with a high density of snags or trees). Bats typically roost in large live or dead trees with loose bark or cavities (Betts, 1998; Crampton & Barclay, 1998; Kalcounis & Brigham, 1998), but it is unknown whether bats roost in dead standing trees after fire.

Timber harvest

Bat foraging strategy is influenced by echolocation call type and wing morphology (Fenton, 1990, 2003), such that some bat species are better adapted to forage in cluttered environments, and others prefer open areas. As a consequence, clearcuts may be suitable foraging habitat for large, fast flying and less manoeuvrable non-*Myotis* bats. In Alberta, Patriquin & Barclay (2003) found that *L. noctivagans*, a larger and less manoeuvrable species, preferred cutblocks and avoided forest interiors, suggesting that clearcut harvesting may facilitate foraging activity. However, smaller *Myotis* bat species generally avoided flying across large open areas (Lunde & Harestad, 1986; De Jong, 1994) such as clearcuts, and instead concentrated their

foraging effort along block edges (Crampton & Barclay, 1998). *M. lucifugus* and *M. septentrionalis* foraged along forest or residual edges in Alberta, and were least active in the middle of cutblocks (Hogberg, Patriquin & Barclay, 2002). Although bats may use clearcuts for foraging, the availability of suitable roosts is likely the limiting factor for persistence of bats populations; clearcuts without live trees do not provide roosting habitat and hence will not likely support resident bat populations.

Establishment and aggradation stages

Bats forage in young burned establishment stage stands, but activity is generally lower in these stands than in old-growth stands (Crampton & Barclay, 1998). Burned stands within the aggradation successional stage provided relatively poor habitat for bats. Crampton & Barclay (1998) found that bats did not roost in 50- to 65-year-old mixedwood stands, and that bats exhibited low activity in these stands relative to older stands. Mature stands tended to be too cluttered for foraging for most species, and lack cavity-bearing trees for roosting. No studies were found that examined bats' use of harvest-origin stands in the establishment or aggradation stage.

Old growth stage

Most bat roosts have been found in large-diameter trees, often in a state of decay, in old uncluttered stands (Campbell, Hallett & O'Connell, 1996; Callahan, Drobney & Clawson, 1997; Betts, 1998; Crampton & Barclay, 1998; Zielinski & Gellman, 1999). The cavities thus formed provide escape cover and an ambient temperature suitable for bat thermoregulation (Kalcounis & Brigham, 1998). In addition to providing roost sites, the structure of old-growth stands is also more conducive to bat movement. Old stands have less clutter because of high canopy, low tree density and abundant forest gaps that create spatial heterogeneity favoured by bats (Crampton & Barclay, 1998).

Bats exhibited higher foraging activity in old mixedwood stands than in young or mature stands, and all roost trees were located in old stands (Crampton & Barclay, 1998). In Ontario, silver-haired bats and hoary bats were significantly more abundant in old-growth white pine mixedwood stands than in mature mixedwood or selective logged stands (Jung *et al.*, 1999). An analysis of forest attributes showed that *Myotis* species responded to intact stands with an open understorey and closed canopy; non-*Myotis* species responded positively to canopy gaps and super-canopy trees (Jung *et al.*, 1999). In California redwoods, old-growth forest is suggested to be a vital component of bat habitat (Zielinski & Gellman, 1999). In Pacific Northwest hemlock forests, bat activity was higher in old-growth stands than in mature (50–100 years old) stands (Humes, Hayes & Collopy, 1999). Thomas (1988) also found that bat activity in the Pacific northwest was greater in old-growth stands (>200 years) than in mature (100–165 years) or young (<75 years) stands. In the boreal forest, bats preferred deciduous trees for roosts (Crampton & Barclay, 1998; Kalcounis & Brigham, 1998); however, bats were more active in mixedwood stands than in aspen or jack pine stands (Kalcounis *et al.*, 1999).

Live residual trees

Erickson & West (2003) suggested that, based on observed relationships to forest structure, bats should be able to use stands of any seral stage, provided the appropriate roosting structure – trees and snags – were present. Patriquin & Barclay's (2003) findings indicate that residual trees left behind selective logging (thinning) provide marginal immediate advantages to foraging bats, but suggest that thinning is more beneficial to bats in the long term than are clearcuts, due to accelerated convergence to pre-disturbance states.

LAGOMORPHS

Initiation stage

Forest fire

The use of recent burns by snowshoe hares *Lepus americanus* is minimal, as they require dense understoreys (Conroy, Gysel & Dudderar, 1979; Wolfe *et al.*, 1982; Litvaitis, Sherbourne & Bissonette, 1985a,b; Férron & Ouellet, 1992), adequate vegetative structure (Férron & Ouellet, 1992), and habitat interspersion (Conroy *et al.*, 1979), all of which are reduced after fire. Hare habitat use has been correlated with shrub cover density when shrub heights are over 1 m (Wolfe *et al.*, 1982; Pietz & Tester, 1983); the shrub layer provides thermal cover and protection from predators (Wolff, 1980; Buehler & Keith, 1982). Consequently, hares generally avoid large open areas (Pietz & Tester, 1983; Férron & Ouellet, 1992), such as burned stands.

Timber harvest

Snowshoe hares seldom occur in harvested stands at this successional stage, because of the lack of suitable understorey cover. Snowshoe hares are absent or uncommon in clearcuts as they are postfire (Hooven & Black, 1976; Burgason, 1977 in Litvaitis *et al.*, 1985b, Férron, Potvin & Dussault, 1998). Thompson *et al.* (1989) found that hare tracks were least abundant in recent (<5 years old) clearcuts compared to older harvested and uncut stands. Limited hare activity in recent cutblocks is presumably due to lack of winter browse (Monthey, 1986); activity tends to be restricted to edges where dense understorey is available (Conroy *et al.*, 1979). In the southern boreal forest, Férron *et al.* (1998) found that hares had not returned to clearcuts after 4 years, and predicted that black spruce habitat would not be suitable until at least 10 years after logging. Similarly, Burgason (1977) found that hares began to return to cuts with regenerating spruce-fir after 6–7 years, reaching peak densities after 20–25 years.

Establishment stage

Forest fire

Habitat becomes increasingly suitable for snowshoe hares throughout this successional stage. The amount of understorey development in young stands is ideal for both foraging and cover; understorey density has been positively associated with hare overwinter survival and spring population densities (Litvaitis *et al.*, 1985b). Shrub heights over 1 m (Wolfe *et al.*, 1982; Pietz & Tester, 1983) make these stands highly suitable for hares. In Alberta, hares were the most abundant small mammal species in 20- to 30-year-old mixedwood stands, and were more abundant in this stand age than in mature- or old-growth stands, exhibiting a strong association for young stands (Roy *et al.*, 1995). Furthermore, hare density was positively related to density of small trees, shrubs, saplings and willow, and was negatively related to density of large trees. Dense deciduous shrubs may be used as winter habitat (Wolff, 1980), but these stands typically provide marginal habitat when snow accumulations are large (Wolfe *et al.*, 1982). In general, winter hare activity is higher in coniferous stands of this age than in deciduous stands, because of superior thermal and protective cover, although aspen-conifer edges may be used (Wolfe *et al.*, 1982).

Timber harvest

As with postfire stands during this successional stage, cutblocks gradually become more suitable for hares because of increasing vegetative cover. Monthey (1986) observed that snowshoe hare activity was greater in 12- to 15-year-old cutblocks than in 7- to 9-year-old cutblocks, and hare activity should return to high levels in 20–30 years post disturbance

depending on the rate of growth and type of tree species in clearcuts (Burgason, 1977; Férron *et al.*, 1998). Thompson *et al.* (1989) found that snowshoe hare tracks were most abundant in the 20+-year age class compared to younger, older and uncut stands. Coniferous stands may provide greater thermal and protective cover during winter, and consequently hare activity is usually greater in coniferous stands than in aspen stands (Wolfe *et al.*, 1982). Hares also use dense deciduous shrubs during winter, and may switch to more open range during summer, relying on habitat interspersion to meet seasonal needs (Wolff, 1980).

Aggradation stage

Hare abundance decreases as stands mature, as evidenced by low abundance in 50- to 65-year-old mixedwood stands (Roy *et al.*, 1995). In Canada's southern boreal forest, mature conifer and deciduous stands with sparse understoreys constituted low-utilization sites by snowshoe hares (Férron & Ouellet, 1992). In harvested stands, Thompson *et al.* (1989) found that hare tracks were most abundant in the 20+-year-old age class, and still significantly higher in 30+ years than in younger cut sites and uncut stands. Hares were found to be abundant in 40-year-old mixedwood stands in Newfoundland (Thompson & Curran, 1995). While hares are abundant at the beginning of this successional stage, they decline as canopy closure increases and understorey cover decreases.

Old growth stage

Hares use old-growth stands, but habitat is less suitable than in younger stands. In mixedwood stands, hares were significantly more abundant in young (20–30 years old) stands than in either mature or old stands (Roy *et al.*, 1995). While food may be available in older stands, cover may be inadequate because of a reduced understorey.

UNGULATES

Initiation stage

Forest fire

Caribou *Rangifer tarandus* feed primarily on lichen; this is often their sole food source in winter. Fire often destroys lichen growth within burns (Morneau & Payette, 1989). Caribou forage is augmented by shrubby vegetation in summer (Rettie, Sheard & Messier, 1997); although young burns may be an abundant source of regenerating vegetation for summer browse, the lack of lichen for winter forage tends to make these areas unsuitable for caribou, often prompting caribou to abandon burned sites (Schaefer & Pruitt, 1991). As well, deadfall accumulating in young burns provides movement barriers. Accumulation is prevalent *ca.* 5 years after burning, making this age-class stand unusable for caribou in some instances (Schaefer & Pruitt, 1991). Despite these issues, and a known preference for mature forests (Chubbs *et al.*, 1993; Arseneault *et al.*, 1997), a study in British Columbia found that caribou selected burns and sites with regenerating woody vegetation in the spring (Boonstra & Sinclair, 1984). Any response to fire is likely to be short-term and with minimal impact on populations, as caribou tend to have large home ranges, and even sedentary woodland herds will shift in space according to habitat and environmental conditions (Mahoney, 2000). Interestingly, fire may have long-term beneficial consequences. Old-growth stands (>150 years) tend to exhibit replacement of lichens with feather mosses; fire restarts succession and may act to keep lichen-dominated mature forests on the landscape (Schaefer & Pruitt, 1991).

In general, other ungulates, including moose *Alces alces*, white-tailed deer *Odocoileus virginianus*, black-tailed or mule deer *O. hemionus*, and elk *Cervus elaphus*, make use of

young seral stages – sites with regenerating trees, shrubs and grasses – for foraging (Bergerud & Manuel, 1968; Cairnes & Telfer, 1980; Cederlund & Okarma, 1988; Pearson *et al.*, 1995; Collins & Schwartz, 1998). Historically, fire has been a key disturbance factor maintaining young seral stages of vegetation favoured by moose (see Krefting, 1974 and Spencer & Hakala, 1964 for reviews). In Alaska, moose occupied sites immediately following fire, and used them more than expected up to 4 years post fire (Gasaway *et al.*, 1989; see also MacCracken & Viereck, 1990). Moose with limited exposure to a burned site, prefire, shifted their home ranges to include those sites, post fire. When an area within a moose home range burned, the time spent by that moose in these burned locales increased (Gasaway *et al.*, 1989). The rate at which browse regrowth occurs is an important predictor of moose abundance post fire. Aspen stands in Alaska contained abundant browse within 2 months post fire, and moose utilized these burns the first postfire winter. These aspen stands produced 10 times as much browse as spruce/birch stands 130+ years old (MacCracken & Viereck, 1990).

Elk make use of the abundant forage in burned sites as well. In Yellowstone, elk grazed on aspen suckers that occurred abundantly in young burn sites, although there were no differences in browsing intensity between burned or unburned sites (Romme *et al.*, 1995). Pearson *et al.* (1995) found elk used <10-year-old burn sites more often than expected, although this changed seasonally. Interestingly, the spatial arrangement of burned area on the landscape did not influence elk use or grazing intensity (Pearson *et al.*, 1995), suggesting that this is a stand-level selection process. Young burns also provide regenerating forage for white-tailed deer, although they prefer some escape cover (Kearney & Gilbert, 1976; Lyon & Jensen, 1980). Excessive DWM in burns may discourage their use (Lyon & Jensen, 1980).

Timber harvest

In Newfoundland, Mahoney & Virgl (2003) found that clearcuts in this stage were utilized by caribou significantly less than other stand ages. Another Newfoundland study observed that 50% of collared caribou moved away from timber harvesting operations, but returned 1 year post cut (Chubbs *et al.*, 1993). In the subalpine/upper foothills of Alberta, caribou moved away from active cutblocks but part of the herd returned after first-pass logging (Smith *et al.*, 2000). However, on average, caribou telemetry locations were significantly farther away from newly harvested cutblocks (1–12 years old) than were random points (Smith *et al.*, 2000), indicating that caribou were actively avoiding these newly disturbed areas. Rettie & Messier (2000) corroborate that caribou tended to use clearcut areas the least in comparison to other boreal habitat types, with few exceptions. Some herds selected for clearcuts relatively more often, but this selection changed seasonally. This seasonality was most likely in response to shifts in forage availability – caribou are more likely to occupy a cutblock if lichen is still present in adequate amounts (Rettie *et al.*, 1997). Lack of ground treatment during harvesting operations preserves lichen growth and facilitates lichen regeneration. Although DWM may inhibit caribou movement in clearcuts, it also fosters the hydric microclimate necessary to foster lichen regrowth and hence support caribou occupation.

In the presence of fire suppression, forest harvesting has become the most consequential disturbance regime maintaining moose forage (see Krefting, 1974 for review). Moose make extensive use of young clearcuts, selecting them over other habitat types (Cederlund & Okarma, 1988; Heikkilä & Härkönen, 1993; Crête *et al.*, 1995). Moose numbers are known to increase significantly with amount of harvesting in the landscape (Forbes & Théberge, 1993). In Newfoundland, moose grazing of regenerating balsam fir in cutblocks is so extensive that growth is prevented, and spruce regenerates instead (Bergerud & Manuel, 1968; Thomp-

son & Curran, 1993). Retarded regeneration also exists in moose-browsed pine cutblocks in Scandinavia (Lavsund, 1987; Edenius *et al.*, 2002). A study of moose browsing intensity in cutblocks of different ages and sizes indicated that cuts aged 7–10 years provided the most winter forage; within this age range, cutblocks 4–50 ha in size were utilized most by moose (Thompson & Curran, 1993). Thus, abundance of forage is not the sole predictor of moose usage of new cutblocks; distance from edge and available cover also influence moose presence. In Ontario, moose with calves avoided younger cutblocks (Thompson & Vukelich, 1981), suggesting cover may be particularly important when young are present. Even when moose do select closed-canopy stands, a higher percentage of logging at the landscape level supports more moose (Forbes & Théberge, 1993), indicating that habitat selection at scales beyond the stand influences moose abundance in forested areas.

Other ungulates make use of regenerating browse and grasses in young clearcuts as well, although escape cover plays an important role. As well, both white-tailed and black-tailed deer respond negatively to excessive slash left in cutblocks (Lyon & Jensen, 1980). Black-tailed deer use aspen cuts, although cutblocks are not necessarily selected (Collins & Urnes, 1981; Kirchoff & Schoen, 1983; Kremsater & Bunnell, 1992). In Alaska, Wallmo & Schoen (1980) found that black-tailed deer made more use (as determined by pellet counts) of uneven-aged old-growth coniferous forests than young coniferous clearcuts, or mature second-growth stands, although this may not be the case in aspen or mixedwood systems.

In contrast, white-tailed deer in Montana made use of young cutblocks, selecting a regenerative stage representing a trade-off between cover and forage (Lyon & Jensen, 1980). St-Louis *et al.* (2000) found that white-tailed deer made extensive use of young cutblocks when felled trees provided browse during the winter, although deer did not change their home range to exploit these areas. White-tailed deer preferred small cutblocks with high edge-to-area ratios (Tomm, Beck & Hudson, 1981). These spatial characteristics were significant predictors of white-tailed presence whereas forage was not, suggesting a reliance upon cover.

Elk graze upon aspen suckers in young cutblocks (Romme *et al.*, 1995) but preferred well-established cover within them (Lyon & Jensen, 1980). Edge, Marcum & Olson, (1985) found that elk did not significantly shift the size, location or fidelity of their home ranges in response to logging activity within them.

Establishment stage

Forest fire

Schaefer & Pruitt (1991) found caribou avoided sites 5–37 years post burn because of inhibition of movement by DWM. In contrast, moose are found in comparatively high densities in 11+-year-old burned stands (Schwartz & Franzmann, 1989), although abundance is decreased from that in <10-year-old stands (Cederlund & Okarma, 1988; Crête *et al.*, 1995). Thompson & Vukelich (1981) found that this age class of burn was used by moose less than expected by availability. Moose reproductive rates at this stage were significantly higher – 70% vs. 22% – than in older (30+ years old) burns (Schwartz & Franzmann, 1989), although there was no difference in calf survival between the two age classes. Lautenschlager *et al.* (1997) found that 14-year-old burns produced more moose forage than did 60- to 80-year-old forests.

The frequency of occurrence of white-tailed deer, black-tailed deer or elk is expected to increase with forest succession – a trade-off between cover and forage availability (Lyon & Jensen, 1980). Johnson *et al.* (1995) suggested that in the southern Appalachians, white-tailed deer abundance is lower at this successional stage when crown closure reduces the availability

of browse, and canopy gaps have not yet formed. However, the applicability of this assumption to boreal stands is unknown.

Timber harvest

Caribou select stands <20 years old significantly less than older stands (Mahoney & Virgl, 2003). Moose are less abundant in cutblocks at this stage than in 0- to 10-year-old forests, but still greater than in old forests (Cederlund & Okarma, 1988).

Aggradation stage

Forest fire

Removal of lichen by caribou from >50-year-old stands was found to be greater than lichen removal in 1- to 15-year-old or 31- to 50-year-old stands (Arseneault *et al.*, 1997), indicating that stands of this age are more suitable for caribou than younger age classes. Mahoney & Virgl (2003) state that caribou used aggradation stage stands significantly more than they used younger stands; however, aggradation stage stands were used less than were older stands.

Moose abundance decreases at this stage compared to younger stands. Cederlund & Okarma (1988) found that moose avoided mature stands. Although moose were abundant in burned mixedwood at the outset of this age class, they declined dramatically as the stands aged beyond 30 years, and reproductive success dropped (Schwartz & Franzmann, 1989). Lautenschlager *et al.* (1997) noted less forage occurred in 60- to 80-year-old stands than in younger burns.

Timber harvest

Moose in Ontario were found to use cutblocks 25–33 years old more often than expected based on their availability (Thompson & Vukelich, 1981), but no studies of other ungulates were found.

Old growth stage

Data on ungulates' use of old-growth stands are scarce. Caribou tend to be associated with older forests, as there is a steady increase in lichen mat thickness as stands progress from young burns to burns >90 years of age (Arseneault *et al.*, 1997). In Newfoundland, caribou selected old stands significantly more than any other stand stage (Mahoney & Virgl, 2003).

Moose tend to avoid old/mature stands (Cederlund & Okarma, 1988). However, Stelfox, Roy & Nolan (1995) found that moose also made use of old (120+ years) stands, likely exploiting early seral vegetation in canopy gaps. In Alaska, black-tailed deer used uneven-aged old stands much more heavily (as determined by pellet counts) than young clearcuts or managed even-aged second-growth stands (Wallmo & Schoen, 1980). White-tailed deer in Alberta used old (120+ years) stands more in winter than any other successional stage, but did not select for old stands in summer (Stelfox *et al.*, 1995).

Live residual trees

The presence of live residuals after fire or harvest enhances the probability of occupation of cutblocks by ungulate species. Residual trees provide for seedfall or vegetative reproduction (i.e. aspen suckers) that enhance forage regeneration for browsing ungulates. The cover provided by residuals facilitates ungulate use of cutblocks. Moose in Ontario preferred to stay close to hardwood residuals (approximately within 45 m) in young cut areas; browse

surveys indicate that this was not due to food availability, but was more likely due to the presence of escape cover, thermal cover and lower snow depth in the residuals (Mastenbrook & Cumming, 1989). Thompson & Vukelich (1981) also found that residuals facilitated moose movement in cutblocks in Ontario; movements were not made far from conifer residuals. In Montana, elk, white-tailed deer and black-tailed deer all preferred cutblocks with cover over cutblocks without, except where shade inhibited growth of regenerating forage (Lyon & Jensen, 1980).

MUSTELIDS

Initiation stage

Forest fire

American marten *Martes americana* is typically associated with woody cover (Steventon & Major, 1982; Buskirk, 1984; Bateman, 1986), but this predatory mustelid does make use of recent burns to exploit the increase in abundance of small mammal prey. Marten occurred in higher abundance in <10-year-old burns than in older (*c.* 25 years old) burns in Alaska (Paragi *et al.*, 1996). However, demographic analysis indicated that martens in the younger burns were juveniles and transients; this suggests that young burns are population sinks (Pulliam, 1988) for marten dispersing from contiguous unburned source habitats (Paragi *et al.*, 1996). If this is the case, the spatial arrangement of burns on the landscape may play more of a role in marten post-disturbance colonization than within-stand characteristics; burns juxtaposed with unburned habitat will decrease marten abundance on the landscape. This influence of patch arrangement on martens has been documented in clearcut landscapes (Chapin, Harrison & Katnik, 1998).

Data for other mustelids – including short-tailed weasels *Mustela erminea*, long-tailed weasels *Mustela frenata* and fisher *Martes pennanti* – are scant. Like martens, fishers are often associated with abundant woody cover (Arthur, Krohn & Gilbert, 1989; Buskirk & Powell, 1994; Thomasma, Drummer & Peterson, 1991; Badry, Proulx & Woodard, 1997) not found in young successional stages. Simms (1979) found that short-tailed weasels avoided forest interiors and preferred early successional communities.

Timber harvest

Young cutblocks also contain a small mammal prey base exploitable by predatory mustelids. However, most data suggest that clearcuts are avoided, or are suboptimal habitat, for larger mustelids. Fishers tend to avoid cutblocks (Arthur *et al.*, 1989) and young seral stages (Weir & Harestad, 1997), and prefer mature forests with high canopy cover and large DWM (Thomasma *et al.*, 1991; Buck *et al.*, 1994; Badry *et al.*, 1997). Martens also avoid young cutblocks. In southern boreal Scandinavia, the Eurasian pine marten *Martes martes* avoided young clearcuts (Brainerd & Rolstad, 2002). In Utah, American marten captures were not correlated with prey abundance in logged areas, in spite of high prey biomass (Hargis, Bissonette & Turner, 1999). Martens prefer mature forests with closed canopy cover (Steventon & Major, 1982; Bateman, 1986), although they will enter open areas like clearcuts to forage (Koehler & Hornocker, 1977). Densities of martens in clearcut stands were significantly lower than partial cut or undisturbed stands in Maine (Soutière, 1979). Potvin, Bélanger & Lowell, (2000) found that martens avoided open regenerating cutblocks less than 20 years old. In Newfoundland, martens generally avoided clearcuts <15 years of age without residuals, instead preferring residual stands (Snyder & Bissonette, 1987). However, it should be noted that some martens were trapped in this age-class clearcut, and that these martens were resident adults, not juveniles or transients. This indicates that clearcuts may be usable by

martens, but in very low densities (Snyder & Bissonette, 1987). In Ontario, Thompson (1994) found that marten densities were *c.* 90% higher in uncut forests than in logged forests 0–30 years old. Martens in those uncut areas were older than those living in logged areas. Martens rarely stayed in deciduous stands longer than 1 years post harvest; those that did were often younger, experienced higher mortality (Thompson, 1994), and had lower hunting activity and success rates (Thompson & Colgan, 1994). These results suggest that young clearcuts might be acting as population sinks for martens. It should be noted that the landscape pattern of cuts also influences marten distribution; martens were nearly absent from landscapes where >25% of the land base was harvested (Hargis & Bissonette, 1997; Hargis *et al.*, 1999).

In contrast to these larger mustelids, short-tailed weasels, particularly females, made extensive use of young aspen cutblocks in Alberta (Lisgo, 1999); short-tailed weasels foraged in cutblocks and used slash piles and tree bases as resting sites. Thompson (1988), using track counts, recorded high abundance of short-tailed weasels in young clearcuts. In British Columbia, *Mustela* spp. were captured more in young clearcuts than in forested stands; this was thought to be linked to a large prey base in clearcuts (Sullivan *et al.*, 1999). Thompson *et al.* (1989) found no consistent pattern in short-tailed weasel abundance over different successional stages. No data could be found on long-tailed weasels' response to clearcutting, but their ability to utilize a broad range of open natural and anthropogenic habitats (Proulx & Drescher, 1993) suggest they may be able to exploit clearcuts and the small mammal prey occurring there.

Establishment stage

Forest fire

In the only available reference on mustelid use of burns of this age class, Latour, Maclean & Pool (1994) observed that martens in Northwest Territories included 21-year-old spruce burns in home ranges that also included unburned forests. However, these burned areas were used less than expected based on their availability.

Timber harvest

Martens avoided 16- to 23-year-old cuts in both summer and winter in Newfoundland (Snyder & Bissonette, 1987). In Ontario, Thompson (1994) found that marten densities were *c.* 90% higher in uncut forests than in logged forests 0–30 years old, and that martens in uncut areas were older than those living in logged areas. Mortality rates were higher in logged areas than in unlogged areas. In Quebec, Potvin & Breton (1997) found that marten home ranges included 20-year-old clearcuts, but that these ranges were twice as large as ranges without them. This indicates that this age stand represents poor-quality habitat, as maintaining a larger home range exacts higher energetic costs. Potvin & Breton (1997) found that martens in 1- to 20-year-old harvested landscapes exhibited higher natural mortality and dispersal rates. Short-tailed weasel abundance in clearcuts of this age was lower than in initiation stage clearcuts in Ontario (Thompson, 1988).

Aggradation stage

Martens were less abundant in burns 25–28 years old than in <10-year-old burns, which was attributed to the instability of the small mammal prey base in the older areas (Paragi *et al.*, 1996). Similarly, martens were found rarely in harvested second-growth 40- to 60-year-old stands of balsam fir in Newfoundland, preferring older stands (Thompson & Curran, 1995). This difference was not due to canopy cover, but to differences in structure on the forest floor

that provide habitat for meadow voles, an important food source for martens in that province (Thompson & Curran, 1995).

Old growth stage

Marten tracks were most abundant in uncut (150–200 years old) stands than in any other age class of harvested stands studied (ranging from 0 to 30+ years old) (Thompson *et al.*, 1989). Martens in Ontario were found in old uncut stands at densities 90% greater than in cut stands (Thompson, 1994); these martens were older and had lower mortality rates than those in younger logged stands (Thompson, 1994). Sturtevant, Bissonette & Long (1996) reviewed and modelled marten habitat requirements, they suggested that vital elements of marten habitat are found within over-mature stands. All of these studies indicate that the 76- to 125-year seral stage is important habitat for marten populations. Similarly, in southern boreal Scandinavia, Brainerd & Rolstad (2002) found that Eurasian pine martens preferred 80+-year-old conifer stands with trees >20 m in height. Data are unfortunately absent for other mustelids, although fishers are generally recognized as old-growth forest species (Arthur *et al.*, 1989; Thomasma *et al.*, 1991; Buskirk & Powell, 1994; Badry *et al.*, 1997).

Live residual trees

Cutblocks and burns with residuals may harbour more mustelid species. Fisher and marten tend to prefer some woody canopy cover (Koehler & Hornocker, 1977; Steventon & Major, 1982; Buskirk, 1984; Bateman, 1986; Snyder & Bissonette, 1987; Arthur *et al.*, 1989; Thomasma *et al.*, 1991; Badry *et al.*, 1997), so the presence of residuals should also facilitate occupation of the cutblock. Extensive studies on marten, in particular (e.g. Soutière, 1979; Snyder & Bissonette, 1987; Chapin *et al.*, 1998; Hargis *et al.*, 1999; Potvin *et al.*, 2000), corroborate the importance of skips and residuals to survival and reproduction.

CANIDS, FELIDS AND URSIDS

Initiation stage

Forest fire

Few data exist on the use of young burns by canids (including red fox *Vulpes vulpes*, coyotes *Canis latrans*, and wolves *C. lupus*), felids (including Canada lynx *Lynx canadensis*) or ursids (including black bears *Ursus americanus* and grizzly bears *Ursus arctos horribilis*). Coyotes and wolves are known to inhabit open or diverse areas (Ballard & Dau, 1983; Dekker, 1983; Harrison, Bissonette & Sherburne, 1989; Koehler & Hornocker, 1991; Gese, Ruff & Crabtree, 1995; but see Mladenoff, Sickley & Wydeven, 1999). However, wolves in Alaska tended to avoid burned stands for 2 years post fire, but used those areas 3 years post fire (Ballard *et al.*, 2000). Wolves' use of the area shifted seasonally (Ballard *et al.*, 2000), possibly in conjunction with shifts in prey base. Red foxes were observed in conifer burns in Quebec (St-Georges *et al.*, 1995) although no analysis of preference or avoidance was conducted. Foxes and coyotes occur in fragmented landscapes, suggesting they might benefit from forest disturbance (Oehler & Litvaitis, 1996), though no studies have explicitly addressed young burns.

When foraging, black bears preferred aspen stands over open areas, because of the higher abundance of food-producing shrubs in aspen (Pelchat & Ruff, 1983). Black bears made use of young regenerating forests for foraging, but when denning, preferred mature forests to regenerating ones (Tietje & Ruff, 1980). This was most likely due to the lack of large, overturned, windblown trees in newly disturbed areas. The creation of early climax habitat by fire had a positive impact on grizzly bears by increasing availability of preferred foods (Hamer, 1996).

Timber harvest

In boreal Ontario, Thompson *et al.* (1989) found that the abundance of red fox tracks was higher in 0- to 5-year-old clearcuts than in uncut stands. Lynx tracks were rarely found in recently harvested stands (Thompson *et al.*, 1989).

Establishment stage

Forest fire

Fox abundance was positively related to burned forest regenerating to conifer (St-Georges *et al.*, 1995), although the effect of burn age is unknown. Wolves have been observed using a 15-year-old burned site on an occasional basis (Théberge & Pimlott, 1969). Wolf density in Alaska was high in large burns 11+ years old, but was not significantly different from burns 30+ years old (Schwartz & Franzmann, 1989). Schwartz & Franzmann (1989) found that black bear adult mean weight, reproductive success and cub survival was greater in 11+-year-old burns than in 30+-year-old burns.

Timber harvest

Thompson *et al.* (1989) found that red fox tracks were more abundant in the 10+-year age class than in younger clearcuts or in uncut stands (Thompson *et al.*, 1989). Coyotes were found to select regenerating cutblocks of this age in winter (as well as mature conifer) (Parker & Maxwell, 1989). Lynx tracks were more common in the 20+ age class than in younger, older or uncut stands (Thompson *et al.*, 1989). High lynx abundance correlates with high snowshoe hare abundance in this age class, as lynxes are more closely linked with prey abundance than with forest structure. Grizzly bears in Montana avoided cutblocks 16–35 years old, but made use of the habitat immediately adjacent to the blocks (Zager, Jonkel & Habeck, 1980).

Aggradation stage

Forest fire

Wolf density in the early aggradation stage was high but not different from 11+-year-old burns (Schwartz & Franzmann, 1989). In the Northwest Territories, lynxes were found to select for dense coniferous habitat in this successional stage where snowshoe hares were abundant (Poole, Wakelyn & Nicklen, 1996), but Thompson *et al.* (1989) found fewer lynxes in the later years of this stage than in establishment stage stands. Grizzly bears preferred 35- to 70-year-old burns more than older stands, presumably because of the relatively higher abundance of forage and cover provided by the subcanopy in the more recently disturbed areas (Zager *et al.*, 1980).

Timber harvest

Red fox tracks were significantly more abundant in 30+-year-old regenerating stands than in uncut stands (Thompson *et al.*, 1989). Although wolves might be expected to exploit prey populations found in cutblocks of this age, no differences occur in diets of wolves in logged or unlogged areas (Kohira & Rexstad, 1997). Lynx tracks were more abundant in 20- to 30-year-old stands than in younger, older or uncut stands (Thompson *et al.*, 1989).

Old growth stage

Red fox tracks were less abundant in uncut stands than in regenerating stands 0–30+ years old (Thompson *et al.*, 1989), indicating that they favour the younger successional stages, most likely because of the higher abundances of prey items occurring there. Lynx tracks were rarely

found in uncut stands (Thompson *et al.*, 1989), likely because of the paucity of snowshoe hares found there.

It should be noted that paucity of data on the response canids, felids and ursids to stand structure, or prey availability, throughout successional time represents a serious data gap; predators may have a significant impact on prey species and their response to forest disturbance at the stand level.

DISCUSSION

Following fire or timber harvest, the abundance of red squirrels, flying squirrels, hares, bats, mustelids, canids and caribou generally decreases. For some of these mammalian species groups, recovery to pre-disturbance states does not occur until stands reach the old growth stage a century or more later (Table 1).

The response of mice and voles to fire and timber harvest varied considerably between studies. In general, all small mammal species recolonize burns and cutblocks to some degree soon after disturbance. Diversity and species dominance varies throughout succession, with generalist species dominant in early successional stages, and specialist species becoming dominant in later stages. Abundance of each species varies considerably, but when a decline in abundance does occur, it is largely due to a reduction in moisture and thermal cover, a result of the changes to DWM and herb and shrub layers.

Red squirrels and flying squirrels are consistently sensitive to forest fire and harvest. The mature cone-bearing or senescent trees upon which they rely for food and denning are generally absent immediately post disturbance, leaving little suitable habitat. Although red squirrels increase in abundance the first few decades after disturbance, these are generally juvenile non-reproductive individuals; these individuals typically indicate poor red squirrel habitat quality (Wheatley, Larsen & Boutin, 2002). Flying squirrel abundance generally stays low through the establishment and aggradation stages until regenerating or remnant trees start to senesce. Red squirrel and flying squirrel abundance peak in old growth stages with the occurrence of mature seed-bearing and decaying trees, as well as abundant fungal and lichen growth.

Species dominance in the bat community changes through successional time after disturbance. Larger, less manoeuvrable non-*Myotis* bats prefer clearcuts to mature forest interiors, but smaller, more manoeuvrable *Myotis* bats are much reduced in abundance in clearcuts. Activity for all species of bats appears low in establishment and aggradation successional stages, though data are scarce. Bat abundance peaks in old-growth stands. The presence of large-diameter old senescent trees provides roosting habitat, and abundant forest canopy gaps in old-growth stands provide foraging habitat, for both large and small bat species.

Snowshoe hare abundance is extremely low immediately following fire and harvest, as the small shrubby vegetation preferred by hares is typically absent. Hare abundance increases rapidly and peaks in the establishment stage, when regenerating vegetation provides ample forage and cover. As the forest canopy closes through successional time the shrub layer decreases, and so does hare abundance, which is typically low in aggradation and old growth stages.

Moose, white-tailed deer, black-tailed deer and elk forage for the young successional browse in young cuts. Initiation and early establishment successional stages often house the highest abundances of these species. However, these ungulates can also be negatively impacted by the lack of cover afforded in open cutblocks; therefore demographic characteristics such as survivorship and reproduction rates may increase in mid-successional stages, where a

compromise between adequate cover and forage is achieved. The exception is caribou, which are largely absent from burned and harvested stands following disturbance. Caribou abundance increases slowly through successional time, corresponding to increased lichen growth as stands age. Caribou abundance peaks in old-growth stands.

The effects of reduced canopy are cumulative as one moves up the trophic pyramid. As prey species abundance changes in response to disturbance, the reduction in prey biomass and availability compounds with the lack of canopy (escape) cover for their predators. Marten juveniles are present in young burns, but adult marten and fisher avoid young clearcuts. Short-tailed weasels use young clearcuts; data for other species are scarce. Marten and fisher remain in low abundance as stands progress through the establishment and aggradation stages. Abundance of these species peaks in old-growth stands.

Foxes are present in young harvested and burned stands. Their abundance appears to increase through the establishment stage, then decrease as stands become mature, and then old. Wolves avoid burned and harvested stands immediately following disturbance, but occupy these areas to some degree relatively rapidly. Wolves are not abundant throughout succession. Lynxes are rare in young stands, but abundance increases dramatically in establishment stage stands. Abundance remains high in early aggradation stage stands, then decreases as lynxes become rare in late aggradation and old-growth stands. This pattern mirrors abundance of snowshoe hares, the primary prey of lynxes. Black bears and grizzly bears are thought to benefit from early successional stages, but their pattern of abundance through time is unknown.

There are large data gaps for bears, felids, canid and most of the mustelids. Few studies have rigorously assessed the response of these species to forest fire and timber harvest through successional time. This gap is a critical one from an ecological standpoint, as predator-prey interactions are a significant driver of mammalian distribution. Establishing the effects of forest and timber harvest on these predators is fundamental to forming a complete picture of the mammalian community's response to disturbance.

The differences between harvested and burned stands emerging from this review are few. This is due, in part, to the fact that much of the reviewed literature neglects explicit analysis of the amount and pattern of unburned skips, and within-block live residual trees, in disturbed areas. These structural features, when examined, were revealed as important predictors of mammalian use of burned and harvested stands for all mammal species groups. Live residuals infuse DWM, a forest structural element important for small mammals, into the stand. Residuals provide nesting and roosting habitat for bats and arboreal sciurids; reproductively mature trees provide seed forage. Live residual tree canopy provides cover for ungulates and carnivores. Most importantly, live residual trees retained after disturbance age as forest succession occurs, providing old-growth forest attributes before a stand reaches the old growth stage. A more explicit examination of the influence of live residual trees and their influence on recolonization and persistence of mammal species post disturbance is required.

Recommendations

There are two routes (among others) that a harvest management strategy for maintaining biotic diversity could take: (i) mimicking natural disturbance (e.g. forest fire), and (ii) managing for rapid convergence to pre-disturbance states.

The impetus in forestry of late has been to adopt the natural disturbance paradigm and attempt to mimic fire pattern on the landscape. However, this review has shown that large, severe fires without live residuals represent poor sites for mammal recolonization. Mammal

diversity in these sites can be quite low until the aggradation or old growth stages of succession, unless considerable live residuals remain. Mimicking natural disturbance might be a good paradigm to follow in forest wildlife management, but for purposes of mammal conservation, disturbances mimicked should be small with live residual trees and in-stand structure. Ecological processes, such as competition, predation, faecal deposition, browsing and grazing, all converge toward preharvest states much more rapidly with greater percentages of live residual trees.

The natural disturbance paradigm has another fundamental flaw. The conservation of biota intended by the natural disturbance paradigm assumes that the harvest rotation will match a natural fire rotation. If this is not the case, and harvesting pre-empts the life expectancy of an old-growth stand, then mammalian biota will be lost from the landscape. The results of this review confirm that mature and old growth stages are temporally integral to the maintenance of mammalian biodiversity in disturbed landscapes.

An alternative timber harvest management strategy for maintaining mammalian diversity is to maximize the rate of successional convergence to pre-disturbance, old growth states. The following recommendations are geared toward this purpose, with the assumption that the goal is to establish the closest approximation to a preharvest mammalian community within a stand before the next rotation:

1. Leave moderate amounts of DWM on the cutblock.
2. Leave standing dead wood, or snags. These 'legacies' are best kept in proximity to standing live residuals, within a clump. Adjacency of live and dead wood helps provide connectivity between complementary resources and also prevents premature windthrow of snags.
3. Leave a reasonable (>30%) percentage of mature and old live trees as clumped residuals within cutblocks. This is arguably the most critical element in promoting mammal re-occupation post harvest. Without live residuals, many species will be lost from the harvested stand, and will not return for several decades post harvest. With a rapid rotation rate, these species may be lost from managed landscapes in perpetuity.

Our final recommendation is geared toward guiding future research on habitat use by boreal mammals. Although this review focused entirely on stand-level studies, even these reveal that the tendency of most mammal species toward high mobility, and use of large areas, necessitates research and management at both the stand and landscape scales. Although mammals respond to stand structure, landscape structure derived from disturbance will also influence population-level distribution. Forging a link between stand-level responses and landscape-level population dynamics is crucial to understanding the effect of boreal forest disturbance on mammalian biota.

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