

The Ecological Roles of Wildlife Tree Users in Forest Ecosystems

1995



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Province of British Columbia
Ministry of Forests Research Program

Canadian Cataloguing in Publication Data

Machmer, Marlene M.

The ecological roles of wildlife tree users in forest ecosystems

(Land management handbook ; 35)

“This handbook prepared by Pandion Ecological Research Ltd.”--Verso of t.p.

Includes bibliographical references: p.

ISBN 0-7726-2418-6

1. Forest fauna – Ecology – British Columbia.
 2. Forest fauna – Feeding and foods – British Columbia.
 3. Forest insects – Biological control – British Columbia.
 4. Trees – Wounds and injuries – British Columbia.
 5. Forest management – British Columbia.
- I. Steeger, Chrisoph, 1958– . II. British Columbia. Ministry of Forests. Research Branch. III. Pandion Ecological Research Ltd. IV. Title. V. Series.

SB764.C3M32 1995 574.5'2642'09711 C95-960108-2

Prepared by
Pandion Ecological Research Ltd.
P.O. Box 26, Ymir, BC V0G 2K0

© 1995 Province of British Columbia
Published by the
Research Branch
B.C. Ministry of Forests
31 Bastion Square
Victoria, BC V8W 3E7

Copies of this and other Ministry of Forests
titles are available from
Crown Publications Inc.
521 Fort Street
Victoria, BC V8W 1E7

SUMMARY

This report synthesizes North American literature about the effects of wildlife tree users on invertebrate and vertebrate pest populations. The feeding habits of 92 species of wildlife tree users in British Columbia are described along with the forest pest species (vertebrate and invertebrate) they prey on. By examining the trophic relationships of wildlife tree users, knowledge of their other ecological roles is gained. These roles are identified and discussed in the context of forest management. Management recommendations and research directions are discussed.

Wildlife tree users are arranged into foraging guilds, and studies that investigate the effects of individual species or entire guilds on the abundance and distribution of forest pests are reviewed. These effects are quantified when possible and anecdotal information is presented and discussed for guilds where quantitative studies are lacking. This information is used to evaluate the potential capacity of specific wildlife tree users to regulate forest pests in a density-dependent manner.

The impact of wildlife tree users on forest pests is most apparent in the bark-foraging and foliage-gleaning guilds, which have been studied extensively. Members of these groups (e.g., woodpeckers, nuthatches and chickadees) exert a direct influence on pest abundance, exhibiting functional and numerical responses to increases

in pest density. They also affect pest abundance indirectly by altering the microclimate of their prey and by increasing pest susceptibility to other mortality agents such as parasitism, predation, disease and weather. The relative effect of predation by these guilds is greatest at low pest densities; thus they play a significant role in maintaining pests at endemic levels by delaying the onset of outbreaks or by accelerating their decline. The ground- and aerial-foraging (hawking) birds, terrestrial and arboreal rodents, and aerial-foraging and gleaning bats all consume injurious insects. However, the quantitative effect of these wildlife tree-using guilds on pest populations requires further investigation. There is little evidence that vertebrate forest pests are regulated by wildlife tree-dependent carnivorous birds and mammals. However, their actions may reduce pest damage by slowing the rate of an outbreak, accelerating its decline, or interacting with density-dependent factors to lower equilibrium pest densities.

Other ecological roles of wildlife tree users in British Columbia include dispersing mycorrhizal inoculum, seeds and other materials, providing nesting, feeding and roosting opportunities for wildlife, accelerating decomposition in dead and decaying trees, nutrient cycling, transmitting tree and insect pathogens, consuming seeds, and damaging healthy trees.

ACKNOWLEDGEMENTS

We would like to thank Daniel Lousier (Ministry of Forests, Prince George Forest Region) for initiating and supporting this project. Dale Seip (Ministry of Forests, Prince George) provided helpful comments on an earlier version of this document. Professor Oz Garton (University of

Idaho, Moscow), Professor Robert Barclay (University of Calgary) and Grant MacHutchon supplied background reference material. Joan Siderius assisted with information gathering. We also thank Susan Bannerman for her thorough editing of the manuscript.

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1 INTRODUCTION

Wildlife trees are an integral component of forest ecosystems and have become the focus of integrated forest management in British Columbia. A wildlife tree is “a tree (dead or alive) which provides present or future critical habitat for maintenance or enhancement of wildlife” (Backhouse and Lousier 1991). Its value for wildlife may be provided by one or more physical attributes such as structure, age, condition, species, geographic location or surrounding habitat features. In British Columbia, more than 90 wildlife species, or approximately 16% of the province’s indigenous birds, mammals and herptiles depend to some extent on wildlife trees for reproduction, feeding or shelter (Backhouse and Lousier 1991).

The forest’s potential to produce and retain wildlife trees can be eliminated by intensive forest management and silvicultural practices (e.g., clearcut harvesting, short harvest rotations, even-aged stand management, and multiple thinning), snag and associated Workers’ Compensation Board safety regulations, fire-prevention activities, and public gathering of firewood (McClelland 1979; Thomas et al. 1979, Cline et al. 1980; Miller 1985). Consequently, these activities constitute a serious threat to the viability of associated wildlife tree users (Bunnell and Alley-Chan 1984; Raphael and White 1984; Zarnowitz and Manuwal 1985; Lundquist 1988).

The British Columbia Wildlife Tree Committee (WTC) is developing management strategies and a research program to conserve the province’s wildlife tree resource and its dependent wildlife species (Backhouse and Lousier 1991). Part of the interest in conserving these species stems from the potential role that wildlife tree users play in regulating

invertebrate and vertebrate forest pests (Lousier 1989). In this context, pests are species that damage and kill trees. However, it is recognized that these species are natural components of forest ecosystems. The role of insectivorous birds in controlling invertebrate pests has received considerable attention in the European (Bruns 1960; Franz 1961; Herberg 1967) and North American literature (Beebe 1974b; see references in Dickson et al. 1979; Thomas et al. 1979, Takekawa et al. 1982). Much of the information on this topic was collected from other parts of North America and focuses on agricultural systems, on bird species that do not depend on wildlife trees, and on forest ecosystems with different tree and pest species and forest management practices from those occurring in the Pacific Northwest. The relevance of this literature to British Columbia forests requires some clarification.

This report synthesizes North American literature about the effects of wildlife tree users on invertebrate and vertebrate forest pest populations. This is accomplished by:

1. describing the feeding habits of wildlife tree species and the forest pest species (vertebrate and invertebrate) they prey on; and
2. identifying the quantitative effects of wildlife tree users on specific pest prey populations (invertebrates are stressed because there are few quantitative studies on vertebrate pests).

Information about tree species, forest pest species and forest management practices in British Columbia is emphasized. By examining the trophic relationships of wildlife tree users, knowledge of their other important ecological roles is gained. These roles are identified and discussed in the context of forest management.

2 METHODS AND MATERIALS

2.1 General Approach

The literature review covered the following general subject areas:

- diet, food habits, foraging behaviour and consumption rates of wildlife tree species;
- forest pests, forest damage, and wildlife tree species interactions; and
- general ecology, habitat requirements, and forest management of wildlife tree species.

Most of the relevant mammalogy, ornithology, entomology, and wildlife and forest management-related literature was found by searching the Fish and Wildlife and Agricola databases on CD ROM disk. Under each of the three general subject areas, databases were searched for each individual wildlife tree species (common and Latin names), by species guild (e.g., swallows, woodpeckers, owls, etc.), by foraging or nesting guild (bark-foraging birds, foliage-gleaning birds, insectivorous bats, cavity-nesting birds, etc.), by taxonomic guild (e.g., small mammals, raptors, bats), by vertebrate class (e.g., bird, mammal, amphibian), and by larger groupings (e.g., vertebrate). Additional literature was found by consulting a U.S. Forest Service cavity-nesting bird bibliography (Fischer and McClelland 1983). More recent government publications were obtained directly through the Provincial Forest Service library in Victoria.

2.2 Forest Pests in British Columbia

Each year in British Columbia forests are damaged by a variety of vertebrate and invertebrate pest species. These pests cause mortality by reducing tree growth and vigour, thereby negatively affecting forest management and the economic potential of our forests. Predominant invertebrate and vertebrate pests in British Columbia are reviewed elsewhere (Pank 1974; Harestad 1983; Harper and Harestad 1985; Finck et al. 1989; Wood and van Sickle 1991, 1992); however, brief mention of some of the most damaging pests is made here to place

the information compiled about diet into context.

In general, members of the insect orders Coleoptera and Lepidoptera constitute some of the most damaging insects in the province. The mountain pine beetle continues to be the most damaging and bark beetles as a group (mountain pine beetle, spruce beetle, western pine beetle, Douglas-fir beetle, western balsam bark beetle, *Ips* spp., ambrosia beetles, northern spruce engraver beetle, pine engraver beetles, fir engraver beetles) constitute a greater source of tree mortality and economic loss than any other group of forest insects (Wood and van Sickle 1992). Spruce budworm, Douglas-fir tussock moth, western hemlock looper and gray spruce looper have caused the most significant recent defoliation of coniferous hosts over widespread areas in the Interior (Wood and van Sickle 1992).

Many vertebrate species impede reforestation in the province by consuming large quantities of seeds and seedlings, clipping off and browsing seedling shoots, gnawing and stripping the bark, or girdling the boles of sapling or pole-sized conifers. Members of the orders Rodentia and Lagomorpha constitute some of the more damaging vertebrate species with significant losses in young regenerating stands attributed to voles, squirrels, cottontail rabbits, snowshoe hares and porcupines (Sullivan and Sullivan 1982; Finck et al. 1989; Wood and van Sickle 1991, 1992). However, the effect of vertebrate pests is generally negligible when compared to that of insects, disease and abiotic injury. Shrews, mice, pocket gophers, pikas, chipmunks, wood rats, beavers, mountain beavers, deer, elk, moose, black bears and woodpeckers are responsible for only sporadic damage and minor economic losses (Finck et al. 1989).

2.3 Information About the Feeding Habits of Wildlife Tree Users

Species that depend on wildlife trees were arranged into foraging guilds, based on their primary forag-

ing mode and location, and vertebrate class. The following foraging guilds are represented:

- aquatic-foraging birds
- terrestrial-foraging raptors
- bark-foraging birds
- foliage-gleaning birds
- aerial-foraging and hawking birds
- ground-foraging birds
- aerial-foraging and gleaning bats
- terrestrial and arboreal rodents
- carnivores
- ungulates
- amphibians

Some of these designations are not mutually exclusive but they facilitate later discussion of the role of wildlife tree users.

The information about the feeding habits of wildlife tree users was compiled from a variety of sources including original research and many reference texts and guidebooks. Where quantitative data were available, primary foods are listed in decreasing order of their occurrence in the diet (by volume). Only foods that constituted 10% or more of the diet volume in any season are listed. Foods eaten “occasionally” are only included when qualitative data were available. Estimates of the percent animal food or the percent of a certain food type (e.g., insect, fungi) are given when relevant. Whenever possible, primary foods eaten (e.g., insects) are broken down into orders and, in some cases, into families eaten. Specific pest species eaten are included in the comments section of each food habit table in Section 3.1 and in each quantitative study summary table in Section 3.2. A list of the common names and associated taxonomic classification (order and family) of all forest insect pests referred to in the tables is provided in Appendix 1. Common and scientific names of all wildlife tree users are included in Tables 1–9.

2.4 Information About the Regulating Effect of Wildlife Tree Users on Forest Pests

Predators may exert density-dependent regulatory pressure on their prey by increasing their predation efficiency as prey density increases. This increased

efficiency can be achieved in two ways. As prey density increases, predators can respond functionally by attacking more prey or numerically by aggregating or increasing their survival or reproductive rates. Both of these responses were studied by Holling (1959) and their sum is the total number of prey killed by the predator population. Vertebrate predators show functional and numerical responses to some forest insect pests and are capable of exerting direct control over the density of their prey under some conditions (Holling 1959; Berryman 1986).

There are many difficulties associated with studying the effects of insectivorous predators on forest pests. Insects exhibit complex life cycles and the susceptibility of each life cycle stage to the predator and the predator’s response to changes in the density of vulnerable pest stages must be measured. This must be accomplished against a background of several interacting predators, prey, parasites and abiotic factors. For bark-foraging and foliage-gleaning birds, and terrestrial and arboreal rodents, many quantitative studies address a guild’s or a specific guild member’s (the predator) effect on a forest insect pest (the prey). These studies are summarized in Table 10 for avian predators and in Table 11 for mammalian predators. Only studies that explicitly include one or more wildlife tree-dependent species in their predator guild are included in these tables. The studies listed in the tables either:

1. investigate the functional or numerical responses of predators to changes in pest species density;
2. estimate the rate of mortality in a pest population attributable to the feeding activity of the predator;
3. quantify the rate of pest consumption by the predator at a known pest density; or
4. combine some of the above.

This information is used to evaluate the effects of specific wildlife tree users on forest pests.

For the other guilds, little quantitative information is available; however, qualitative information pertinent to the potential impact of these guilds on forest pests is presented and discussed.

3.1 Feeding Habits of Wildlife Tree Users

The feeding habits of 92 species of wildlife tree users listed in Backhouse and Lousier (1991) are described in Tables 1–9. The diets of aquatic-foraging birds are listed in Table 1. Five of the nine species take predominantly fish, three of the four remaining species which do eat insects take mainly aquatic forms. Only the Wood Duck feeds on terrestrial insects and these form a small proportion of its summer diet. This group therefore has a negligible influence on forest pest species.

The food habits of 16 terrestrial-foraging raptors are shown in Table 2. Rodents and lagomorphs (e.g., pikas, rabbits, hares) are the most common food of 12 of the 16 species. Vertebrates that can negatively affect forest management and regeneration activities (e.g., voles, mice, shrews, chipmunks, pocket gophers, squirrels, pikas, rabbits, hares and porcupines) are the predominant prey of these 12 species. At least four species (Barn Owl, Northern Hawk-Owl, Spotted Owl and Northern Saw-whet Owl) are considered small mammal “specialists”—that is, small mammals make up more than 90% of their diet volume.

The food habits of bark-foraging birds are listed in Table 3. Terrestrial insects are the “primary” food item (i.e., $\geq 75\%$ of the diet volume) for 11 of the 15 species, and at least 50% of the annual diet volume for the remaining four species. Either Coleoptera or Lepidoptera are the first or second most common insect orders consumed by all species, and 13 of the 15 species are known to prey on various injurious insects (see general comments in Tables 3 and 10). This is most obvious in the Hairy, Three-toed and Black-backed Woodpeckers, all of which consume primarily insects and, in particular, wood-boring beetle larvae of the families Buprestidae (wood-boring metallic beetles), Cerambycidae (wood-boring long-horned beetles), and Scolytidae (bark beetles and ambrosia beetles). Representatives of these insect families are the most injurious insects in temperate coniferous forests (Knight and Heikkinen 1980). The Pileated Woodpecker, Downy Woodpecker, the Williamson Sapsucker and, to some extent, the White-headed Woodpecker feed on members of these families as

well, but they do not specialize as much as the other three species.

Three members of the guild (Williamson Sapsucker, Northern Flicker, Pileated Woodpecker) feed heavily on ants that construct their galleries in moist wood, which weakens trees and increases their susceptibility to windthrow (Knight and Heikkinen 1980).

Larval, pupal and emergent adult stages are all preyed on by the bark-foraging guild and differences in bill morphology and foraging mode between guild members result in the division of insect prey resources. Nuthatches and creepers use superficial foraging techniques (e.g., peer and poke, probe, scale) to chip away bark flakes, locating insect prey on or near the bark surface (Stallcup 1968; McEllin 1979; Franzgreb 1985; Lundquist and Manuwal 1990). Woodpeckers (particularly the Hairy, Three-toed, Black-backed, and Pileated Woodpeckers) use subsurface foraging techniques (e.g., drilling, excavation) to penetrate the subcambium layer where beetle larvae and ants are extracted (Stallcup 1968; Jackson 1970; Connor 1979; 1981; Lundquist and Manuwal 1990). Numerous studies address the effects of this guild on forest insect pests and these are reviewed and their findings discussed in Section 3.2.

Foliage-gleaning wildlife tree users are listed in Table 4. Insects are the most common food item in the diets of all four species and larvae and adults of the order Lepidoptera are ranked first in the diets of three of the four species. This guild consumes various injurious insects.

The food habits of aerial-foraging and hawking birds are listed in Table 5. This guild includes a diverse assemblage of species, and insects constitute the primary food (i.e., $\geq 75\%$ of the diet volume) of 9 of the 10 species. Most members prey exclusively or primarily on flying insects or emergent phases. Five of the 10 species are known to prey on injurious insects. All species are to some extent migratory and their consumption is therefore limited to a fixed breeding period.

The diets of ground-foraging birds are shown in Table 6. The Bewick’s Wren and House Wren eat primarily insects (i.e., $\geq 75\%$ of the diet volume), the Common Grackle is an omnivore and the

House Finch eats mainly seeds and other plant products. Three of the four guild members prey on forest insect pests.

All 12 wildlife tree-dependent bats found in the province are primarily insectivorous (Table 7) and eight of 12 species are thought to prey exclusively on flying insects. Bat diets are correlated with tooth and jaw morphology (Freeman 1981) as well as body size and echolocating abilities (Barclay and Brigham 1991). Strong dentition and muscular jaws are characteristic of species that eat relatively hard-bodied insects (e.g., Coleopterans). Species with small teeth tend to specialize on soft-bodied insects (e.g., Lepidopterans, Dipterans). Small bats are capable of detecting smaller insects, thereby defining the size classes of prey available (Barclay and Brigham 1991). Lepidopterans are the most common insects taken by six of the 12 species and Coleopterans and Lepidopterans make up part of the diet of 11 of 12 species.

Although numerous studies have investigated bat diets using fecal and stomach content analyses (Black 1974; Whitaker et al. 1977, 1981a, 1981b; Warner 1985; Brigham 1990; Brigham and Saunders 1990; Brigham et al. 1992; Whitaker and Lawhead 1992), insects consumed are usually identified by order, and in some cases, by family (Whitaker 1988). There is little information available on the specific forest pest species consumed by bats (R. Barclay, University of Calgary and M. Brigham, University of Regina, pers. comm., February 1993).

The diets of terrestrial and arboreal rodents are listed in Table 8. Diet information was not found for the Sitka Mouse and the Red-tailed Chipmunk. Fungi were the primary food eaten (i.e., $\geq 75\%$ of the diet volume) by three species; they constituted 50% or more of the diet volume in at least six of the 12 species, and appeared as a food item for every guild member. The predominance of fungi in these rodents' diets has far-reaching implications for forest health and productivity. The ecological role of forest rodents in the obligate symbiosis between trees and mycorrhizal fungi is discussed in Section 3.4.1.

Insects are part of the diet in nine of the 10 species for which diet information is available, but insects are the first-ranked food item only for the Deer Mouse and possibly for the Columbia Mouse. Four members of this guild are known to prey on forest insect pests. Their role in controlling these pests is discussed in Section 3.2.3.

The primary foods of eight members of the order Carnivora are shown in Table 9. Small- to medium-sized mammals (rodents and lagomorphs) are the first-ranked foods for five of the eight members listed. The diets of the three remaining species are relatively varied.

The Caribou (*Rangifer tarandus*) and the Clouded Salamander (*Aneides ferreus*) are the only ungulate and amphibian wildlife tree users in the province. Caribou eat lichens, grasses, sedges, shrubs, leaves and other vegetation (Cowan and Guiget 1978). They are unique in their almost exclusive dependence on arboreal lichens in winter (Simpson et al. 1987). The Clouded Salamander eats primarily insects and other invertebrates. Ants, particularly carpenter ants which inhabit moist wood, constitute most of the diet (Orchard 1984).

Fifty-one studies were found that deal explicitly with the impact of the province's wildlife tree users on specific forest insect pests. These studies use a variety of experimental and observational methods to quantify effect: artificial stocking of prey; comparisons of mortality between prey populations of different densities; consumption estimates based on observation, metabolic requirements, digestive rate studies or captive feeding experiments; deterministic modelling; predator exclusion experiments; prey and predator censuses; and predator stomach and fecal content analyses. Eight more quantitative studies pertinent to the topic were found but these failed to identify the specific guild species (Dowden et al. 1953; Morris et al. 1958; Amman and Cole 1983; Campbell and Torgerson 1983; Campbell et al. 1983; Carlson et al. 1984; Takekawa and Garton 1984; Torgerson et al. 1990).

3.2 Regulation of Abundance and Distribution of Forest Pests by Wildlife Tree Users

3.2.1 Bark-foraging birds

Thirty-four studies investigated the impact of guild members on insect pests and 25 of these focused specifically on woodpeckers (Table 10). These studies indicate that bark-foraging wildlife tree users show a density-dependant response to changes in pest population densities. Bark foragers increase the proportion of insects in their diet as the pest populations gradually increase (a functional response: Buckner and Turnock 1965; Koplin and Baldwin 1970; Koplin 1972; Crawford et al. 1983). They also aggregate in pest-infested areas (a

numerical response: Rust 1929, 1930; Baldwin 1960; Buckner and Turnock 1965; Otvos 1965; Mattson et al. 1968; Koplín and Baldwin 1970; Koplín 1972; Crockett and Hansley 1978; Kroll and Fleet 1979; Kroll et al. 1980; Lester 1980; Villard and Beninger 1993). Such aggregations are particularly well documented for woodpeckers feeding on bark beetles. Winter densities can increase up to 85-fold during infestations (Blackford 1955; Yeager 1955; Baldwin 1960; Koplín 1972; Massey and Wygant 1973; Kroll and Fleet 1979; Kroll et al. 1980) and the Downy, Hairy, Three-toed and Black-backed Woodpeckers seem to be the most flexible species in this regard. Observations of 2–12 woodpeckers feeding unhindered at the same tree are not uncommon during such post-breeding aggregations (Baldwin 1960; Koplín 1972). During the breeding season, woodpecker densities can increase up to seven-fold during infestations (Koplín 1972). Factors such as breeding territory requirements, the availability of nesting and roosting sites (snags of sufficient size and suitable decay stage), and food availability between pest outbreaks may limit the size of breeding aggregations (Kroll et al. 1980). During long-term infestations, woodpecker populations also respond numerically (by increased reproduction) to the greater availability of nesting and roosting sites provided by insect-killed trees (Baldwin 1968; Otvos 1979). It is not clear to what extent the fecundity of individual birds can increase during infestations.

The value of the bark-foraging guild in regulating the abundance of their prey populations is enhanced by at least 12 of the 15 bark-foraging species being year-round residents (Campbell et al. 1990). During winter months, these species are the major avian insectivores in forests and their consumption of overwintering pests is an important factor in diminishing the pests', potential for rapid population increase in the spring (Jackson 1979a; Kroll and Fleet 1979). Avian-insect interaction models demonstrate that when insects are exposed to predation over a prolonged period, such as winter, the size of the area of "local stability" (i.e., stable equilibrium densities of predator and prey) can be quite extensive (Otvos 1979).

Predator consumption estimates are given (or could be calculated with available information) in eight studies. Four other studies report the number of prey per predator stomach based on stomach

content analyses but the additional information (e.g., digestive passage rate or number of times the stomach is filled per day) required to calculate daily consumption rates is not given. These data are nevertheless presented for comparisons of relative consumption rates between species. A rough estimate of daily consumption can be calculated by dividing the number of prey per predator stomach by an estimated digestive passage rate (1.2 hours; Takekawa and Garton 1984) and then assuming the bird forages 8–16 hours per day.

Some of the most impressive rates of consumption are shown by woodpeckers. For example, stomachs of Three-toed Woodpeckers contained an average of 915 spruce beetle larvae during an outbreak and woodpeckers are expected to fill their stomachs several times to capacity each day. This could result in an individual consuming many thousand larvae per day (Koplín 1972).

All 34 studies concluded that bark-foraging birds contribute significantly to prey mortality through their feeding activity. The estimated percent mortality in prey populations ranged from 0.5–98%, depending on whether a study took the indirect effects of predator feeding into consideration (see comments in Table 10). This is particularly important in woodpecker predation on bark beetles (Otvos 1979), where birds flake, puncture, excavate and remove bark during the process of feeding. A general reduction in bark thickness changes the microhabitat of the prey and reduces subsequent prey survival. Indirect effects of woodpecker feeding activity on bark beetle mortality include increased parasitism of intact beetle broods (up to 10-fold in winter; Otvos 1965) by parasites with short ovipositors, and increased brood mortality because of the desiccation and lethal temperatures associated with bark thinning (Moore 1972; Otvos 1979). Beetle broods dislodged in bark flakes suffer high mortality as well (Otvos 1965; Kroll and Fleet 1979). The mean density of predatory insects attacking bark beetle broods may decrease (Otvos 1965) or increase (Kroll and Fleet 1979; Kroll et al. 1980) because of woodpecker activity.

Several studies pose the question of whether avian predation complements or diminishes the efficiency of other mortality agents, such as insect predation or parasitism on forest pests. Birds can influence these other mortality agents by:

1. consuming insect predators and parasites directly;

2. preferring or discriminating against parasitized prey; or
3. changing the microhabitat of the prey so that they are more or less susceptible to these other mortality agents (Otvos 1979).

Clearly, woodpecker activity indirectly increases the susceptibility of beetle broods to other mortality agents.

Most avian predators consume beneficial insect predators and parasites; however, their relative frequency in the diet as compared to their availability in trees is usually low (Otvos 1979). Bruns (1960), Buckner and Turnock (1965), MacLellan (1958), Sloan and Coppel (1968), Sloan and Simmons (1973) and Schlichter (1978) all report that birds are highly discriminating in prey selection and that they take a significantly lower proportion of parasitized versus non-parasitized prey.

In addition to their influence on insect predators of bark beetles, woodpeckers may attract or increase the susceptibility of beetle broods to other vertebrate predators through their feeding activity. Brown Creepers and Red-breasted Nuthatches are reportedly drawn to recently "woodpeckered" bark where they can gain access to beetle larvae (Kroll and Fleet 1979; Otvos 1979). It is conceivable that other beetle predators would be attracted by such activity. Birds contribute indirectly to the mortality of their prey by transmitting entomogenous pathogens during feeding (Franz et al. 1955; Bruns 1960; see references in Otvos 1979). All of these indirect effects are not considered in most studies listed in Table 10, but they could substantially increase the prey population mortality rate attributed to the predator.

The rates of prey mortality reported in Table 10 depend on stand-level factors such as density, elevation, and site-specific silvicultural practices. Petit and Grubb (1988) correlated the relatively low mortality rate of hardwood borers in the clearcuts they studied to the dense vegetation and lack of large snags. Woodpeckers were more than two times as prevalent in surrounding uncut forests. Shook and Baldwin (1970) suggested that woodpeckers are more effective at reducing spruce beetles in semi-open stands than in dense stands because more dead and windthrown trees (which attract woodpeckers) are present.

Eleven studies explicitly concluded that the regulatory influence of bark-foraging birds is great-

est at low to moderate prey densities, and this seems to be the case for insectivorous birds in general (McFarlane 1976; Otvos 1979; Holmes 1990). Although this guild exhibits both functional and numerical responses to increasing prey densities, they are unable to keep up with rapidly expanding epidemic prey populations. In two studies, woodpeckers exerted their greatest predatory impact at epidemic prey densities (Koplin and Baldwin 1970; Koplin 1972); however, unusually high levels of winter aggregation are reported in these studies. In general, the reproductive rates, breeding territory requirements, availability of nesting and roosting sites and food supply between outbreaks limit the effectiveness of birds in controlling large-scale epidemic infestations (McFarlane 1976; Otvos 1979; Moeck and Safranyik 1984). The major role of birds is to maintain endemic pest levels, delaying the onset of an outbreak and accelerating the decline in an outbreak that has peaked, which increases the time span between outbreaks (see literature reviews in Buckner 1966; van den Bosch 1971; Beebe 1974b; McFarlane 1976; Otvos 1979; Crawford and Jennings 1982; Takekawa et al. 1982; Fischer and McClelland 1983; Moeck and Safranyik 1984).

3.2.2 Foliage-gleaning birds

Nineteen studies in Table 10 deal with the role of foliage-gleaning wildlife tree users in regulating the abundance of forest pest insects. Members of this guild search for insects on the terminal branches and foliage of conifers and they respond functionally and numerically to increased prey density (Buckner and Turnock 1965; Dahlsten and Herman 1965; Mattson et al. 1968; Gage et al. 1970; Crawford et al. 1983; Crawford and Jennings 1989; Crawford et al. 1990). All species are resident and territorial, and some studies conclude that they are responsible for up to 95% mortality in endemic pest populations (Coppel and Sloan 1971). Suggested limits to the numerical response of this guild are suitable snags for nesting and roosting (Langelier and Garton 1986; Garton 1987).

Although their consumption rates are generally not as high as those of woodpeckers (e.g., 6.1 large western spruce budworm larvae/hour for the Black-capped Chickadee: Garton 1987), foliage gleaners prey on both larval and adult forms and play a major role in reducing defoliation rates and in maintaining sparse populations of western

spruce budworm and other injurious insects (Langelier and Garton 1986; Garton 1987).

All but one of 19 studies concluded that this guild plays a role in regulating the abundance of forest pest insects. These birds also probably consume insect predators and parasitoids of their prey in the process of feeding (Otvos 1979) but this effect has not been measured. Members of this guild are known to eat emergent bark beetles (Table 4) and the “in-flight” mortality beetles incur may be significant because it acts on the pre-ovipositing female (see Moeck and Safranyik 1984). Six studies explicitly state that impact was greatest at endemic prey densities. As with bark foragers, members of this guild maintain sparse pest populations between outbreaks but are not capable of stopping an existing outbreak.

3.2.3 Terrestrial and arboreal rodents

Eight quantitative studies were found that investigate the role of wildlife tree-dependent small mammals on forest pests (Table 11). Although consumption estimates (e.g., 400–500 prey per predator per day for red squirrel feeding on spruce budworm) suggest that guild members can potentially consume large numbers of pests, only Holling (1959) and Dowden et al. (1953) concluded that small mammals contribute to pest regulation over a range of prey densities. Four studies are inconclusive and two studies conclude that guild members are not important predators of the prey under investigation. Aside from Hollings’ work, all studies failed to examine predator feeding responses over a range of prey densities and were limited to laboratory observation or trapping a few animals for stomach content analysis. No predator exclusions nor estimates of mortality by predators were attempted. Clearly, the role of small mammals in regulating forest insect pests requires further investigation. Given the impressive consumption estimates attributed to guild members, they may act as a significant density-independent mortality factor, by slowing the rate of pest increase during an epidemic, accelerating the rate of decline of a pest, or interacting with density-dependent factors to produce a lower equilibrium pest density.

3.2.4 Ground-foraging birds

Only one study listed in Table 10 addresses the role of this guild (and the Common Grackle, in particular) in the control of a forest pest (Crawford et al. 1983). Although stomach analyses

indicate that this species feeds on spruce budworm, sample sizes were insufficient to evaluate its effect quantitatively. Two of the four ground-foraging wildlife tree users have relatively broad diets (Table 6) and their potential influence as a group on pest species abundance is probably negligible.

3.2.5 Aerial-foraging and hawking birds

Only two studies were found that investigate the role of specific guild members on forest pests (Table 10). Baldwin (1968) concluded that the Mountain Bluebird and five other species which prey on adult Engelmann spruce beetles were responsible for 24–32% mortality in the population. A mortality rate of 8–26% was estimated for an aerial foraging guild (including the Violet-green Swallow) preying on western pine beetle (Otvos 1979). In both cases, mortality was incurred during the short period of bark beetle emergence, flight and attack on trees and coincided with the nestling feeding period of several of the predator species.

Although other guild members (e.g., Ash-throated and Pacific-slope Flycatchers) have received little attention, Stallcup (1963) observed several unidentified flycatchers (*Empidonax* sp.) eating flying spruce beetles. He estimated the in-flight mortality to be approximately 10%. Similarly, other members of the same genus (e.g., Hammond’s Flycatcher) are significant consumers of spruce budworm moths (Langelier and Garton 1986; Garton 1987).

There are many difficulties in studying the impact of aerial foragers on forest pests. Their consumption is limited to the brief “in-flight” phase of the pest life cycle, and predation is inconspicuous and difficult to quantify without sacrificing the animal. However, mortality incurred by aerial foragers on pre-ovipositing females is considered proportionately more important than that on earlier life cycle stages (Moeck and Safranyik 1984). The quantitative effects of this guild on forest pests merits further investigation.

3.2.6 Terrestrial-foraging raptors

Unlike the relationship between some insectivorous birds that depend on wildlife trees and forest pests, there is little quantitative evidence that raptors can regulate the abundance of their vertebrate prey. Data on their quantitative food intake in the wild and their response to changes in prey availability are lacking for most raptor species (Marti 1987). The most reliable data available are for owls, where

pellet analyses can be used in conjunction with consumption studies on captive birds. Barn Owls are resident small mammal specialists and consume an estimated seasonal average of 60–110 g of whole small mammal prey per day which represents approximately 10–18% of their body weight, or roughly 1.7–3.1 voles (*Microtus* sp.) or 3.1–5.8 deer mice (*Peromyscus* sp.) per day (Marti 1970, 1973; Steenhof 1983). Great-horned Owls consume an estimated seasonal average of 63–119 g of prey per day, which represents 4.7–8.9% of their body weight or 0.33–0.63 adult Red or Douglas squirrels per day (Marti 1970, 1973; Steenhof 1983). These consumption rates are expected to increase during the breeding season with the higher metabolic requirements of incubation, feeding nestlings and fledglings.

Thirteen of the 16 members of this guild are resident (Campbell et al. 1990) and are capable of exerting predation pressure throughout the year. Although there is little evidence that this guild regulates prey in a density-dependent manner, by consuming vertebrate pest species, terrestrial-foraging raptors may slow the rate of an epidemic pest outbreak or accelerate its decline. This group therefore plays a potentially significant role in limiting damage to forests.

3.2.7 Aerial-foraging and gleaning bats

Although it is generally assumed that insectivorous bats play a role in controlling forest pests (Bruns 1960; Ross 1967; Constantine 1970; Hill and Smith 1984), an objective assessment is not possible now because good qualitative and quantitative data are lacking.

Several characteristics of this guild could potentially affect forest pests. Bats are nocturnal hunters so their predatory behaviour can be considered complementary to that of the previous guilds discussed. Lepidoptera is the first-ranked insect order consumed by 6 of the 12 bats in the province that depend on wildlife trees (Table 7) and many are active primarily at night (references in Holmes 1990). Bats of this guild prey mainly on flying insects (Whitaker et al. 1981a) and would be expected to affect mainly the “in-flight” phases of pest life cycles. However, at least four members take flightless insects and spiders (Table 7) and gleaning from the ground or foliage is a well-documented foraging strategy in two of these species (Pallid Bat: Bell 1982; Western Long-eared Myotis: Faure and

Barclay 1992). Bats use prey-generated sound and movement cues as well as echolocation when gleaning (Fenton 1990).

Members of this guild are clearly efficient predators and consume large quantities of insects annually. Juvenile, pregnant and lactating Little Brown Bats consume an estimated 1.8, 2.5 and 3.7 g of insects, respectively, each night (Anthony and Kunz 1977). This amounts to 818, 1136 and 1682 insects per individual per night, respectively, assuming an average prey weight of 2.2 mg (Griffin et al. 1960). Most insectivorous bat species consume between 30–50% of their body mass in insects every night (Anthony and Kunz 1977; Fenton 1990) and wildlife tree-dependent species in the province range from 4.3–27.6 g, on average. Larger species (e.g., Hoary Bat, Big Brown Bat, Pallid Bat) tend to consume larger prey (Anthony and Kunz 1977; Barclay 1985, 1986; Brigham 1990; Brigham and Saunders 1990), so the number of insects consumed per individual per night is expected to be comparable.

Some bat species (e.g., Little Brown Bat, Big Brown Bat, Silver-haired Bat) are known to opportunistically exploit rich patches of prey such as hatches of emergent insects (Buchler 1976; Barclay 1985; Brigham and Fenton 1991; Brigham et al. 1992). It is tempting to speculate that they would behave similarly during pest irruptions or during the emergence phase of certain adult pests but there are no direct empirical data available to support this. Interestingly, a few studies address the strong convergence in foraging behaviour and diet between Big Brown Bats and Common Nighthawks (Brigham 1990; Aldridge and Brigham 1991; Brigham and Fenton 1991). Common Nighthawks are reported to be an important avian predator of the mountain pine beetle (Rust 1929). Stomach analyses showed an average of 76 adult beetles — 20% of the total food volume consumed. It would be interesting to investigate the diet of Big Brown Bats and other guild members in beetle-infested areas during the period of adult emergence, flight and attack.

3.2.8 Carnivores

Data on the rates at which carnivores consume vertebrate pests are lacking. Although some representatives of this guild (e.g., marten, ermine, least weasel) prey heavily on rodents, there is little evidence that wildlife tree-dependent carnivores can

regulate the abundance of their prey. By consuming small mammals, this group may act as a significant density-independent mortality factor, slowing the rate of pest increase or accelerating its decline. This would reduce seed consumption and damage to young, regenerating forest stands.

3.2.9 Amphibians

Because of their dependence on fresh water, amphibians are not considered as important predators of forest insects (Buckner 1966). No references concerning the Clouded Salamander's consumption of specific forest pests were found. The Spotted Salamander, a related species found in the northeastern United States feeds on the late larval stages of spruce budworm (Jennings et al. 1991). However, predation of spruce budworm by this species is considered unimportant when compared with other vertebrate predators (e.g., birds).

3.3 Summary of Impact of Wildlife Tree Users on Forest Pests

Some species that depend on wildlife trees clearly play a role in regulating the abundance of insect pests in forests. This influence is most apparent for the bark-foraging and foliage-gleaning guilds, which have been studied extensively. These groups directly influence prey abundance by consuming large numbers of pest individuals and by altering their foraging and reproductive behaviour with changes in pest density. They also indirectly influence prey populations through their feeding activity, by altering the microclimate of their prey and by increasing prey susceptibility to other mortality agents such as parasitism, predation, disease and weather. Quantitative studies show that the magnitude of these indirect effects is considerable.

It should be stressed, however, that the relative influence of bird predation on pest populations is greatest at low pest densities. Once an epidemic outbreak is established, birds alone are generally unable to control it, unless extremely high levels of predator aggregation overwhelm a very localized infestation. However, insectivorous birds play a significant role in maintaining pests at endemic levels by delaying the onset of an outbreak or by accelerating its decline.

The ground-foraging and aerial-foraging/hawking birds, terrestrial and arboreal rodents, and aerial-foraging and gleaning bats all consume in-

sects and may also have a regulating influence on forest pests, but these groups require further investigation.

Vertebrate forest pests (e.g., voles, squirrels, hares) do not seem to be regulated in a density-dependent manner by carnivorous birds or mammals. Nevertheless, predation by these guilds may cause significant mortality, which reduces the impact of vertebrate pests. Ecologists have debated whether intrinsic or extrinsic factors are the most important in regulating vertebrate prey populations. The general consensus is that the two classes of factors interact to affect prey population abundance (see discussion in Southern 1979).

The discussion of the effects of predators on forest pests has focused only on short-term numerical responses. However, another effect of sustained predatory pressure is evolutionary. Insectivorous bark-foraging and foliage-gleaning birds, because of their regulatory influence on endemic prey populations, have a strong selective influence on their prey that can determine certain traits in their populations. For example, selective predation of defoliating Lepidoptera larvae (Garton 1979) can influence its choice of feeding substrates, feeding schedules, plant species preferences, life history patterns, body pattern and coloration over an evolutionary time scale (see references cited in Holmes 1990). These traits, in turn, determine the pattern and extent of damage by defoliators, so that birds, through selective foraging, indirectly affect other ecosystem components and processes. Because of their quick generation times and high reproductive rates, insects are capable of genetically-based changes over a relatively short time. For example, the peppered moth exhibited a change in the frequency of the melanistic coloration gene from 1–98% of the population within fifty generations (references in Holmes 1990).

3.4 Other Ecological Roles of Wildlife Tree Users

Wildlife tree-dependent species have other important ecological roles in addition to their influence on the abundance and distribution of forest pests. Some of these are perceived as extremely valuable to forest ecosystems whereas others have traditionally been viewed as negative from a forest management and economic perspective.

By transporting and consuming fungi, terrestrial

and arboreal mammals spread mycorrhizal inoculum, which is critical to forest health and nutrition. This same guild, along with seed-eating birds, disperses seeds. Terrestrial and arboreal rodents function as dispersal agents of organic and inorganic materials, increase soil aeration, enhance drainage and ultimately accelerate organic decomposition. All guilds, but most notably birds and bats because of their mobility, contribute to nutrient cycling in forest ecosystems. Primary cavity-nesting and bark-foraging birds provide feeding, roosting and nesting opportunities for other cavity-dependent species as well as increase the rate of tree decomposition.

To some extent, primary cavity-nesters damage healthy trees through their feeding and nesting activities and all forest birds have been implicated in transmitting plant pathogens (e.g., wood-decaying fungi, arboviruses). Some small mammals impede reforestation by consuming seeds and seedlings and by debarking or girdling juvenile trees.

3.4.1 Dispersal of mycorrhizal inoculum

Mycorrhizae are symbiotic associations between fungi and the roots of vascular plants. The fungal hyphae act as extensions of the host's own root system, absorbing nutrients, minerals and water from the soil and translocating them to the host plant. Some mycorrhizal fungi also produce growth regulators that can create new root tips or compounds that enhance the host plant's resistance to pathogens (Maser 1990). In turn, the host supplies sugars produced photosynthetically to the mycorrhizal fungi. Mycorrhizal fungi are thought to occur in 90% of all plant families. Woody plants in the families Pinaceae (e.g., pine, fir, spruce, larch, Douglas-fir, hemlock), Fagaceae (e.g., oak) and Betulaceae (e.g., birch, alder) have developed an obligatory dependence on root-inhabiting fungi to absorb adequate nutrients from the soil (Marks and Kozlowski 1973; Harley and Smith 1983). Experiments show that without mycorrhizal inoculum, commercially valuable tree seedlings (e.g., pine) fail to grow.

The consumption of fungi (mycophagy) by mammals and the strong reliance of some small mammals (e.g., squirrels, chipmunks, voles) on fungi as a primary food source is well documented (Table 8; see also Fogel and Trappe 1978; Maser et al. 1978). This reliance is mutual; small mammals consume primarily (88%) hypogeous fungi, that is,

mycorrhizal fungi which produce their sporocarps (fruiting bodies) belowground (Maser et al. 1978). These fungi lack spore dispersal mechanisms and depend on small mammals for spore dissemination (Fogel and Trappe 1978). Mycophagists consume the sporocarps of mycorrhizal fungi, which contain nutrients, water, viable fungal spores, nitrogen-fixing bacteria and yeast (Maser 1990). These sporocarps emit species-specific odours that attract mycophagists and, once consumed, pass through the digestive tract and are excreted in pellets without loss of viability (Trappe and Maser 1976). The spores from pellets can then contact and inoculate susceptible host roots, being washed into the soil by rain or transported by the tunnelling and burrowing activity of small mammals. Alternatively, germinated spores may fuse with an existing fungal thallus, thereby contributing new genetic material (Maser 1990).

By enhancing the spread of hypogeous mycorrhizal fungi, terrestrial and arboreal rodents maintain their own food supply and disseminate the spores that are critical for the growth and survival of conifers and deciduous hardwoods. Small mammals that feed in forested sites and adjacent clearcuts (e.g., deer mice, chipmunks) aid in reforestation by depositing spore-containing pellets in cutover areas. Seeds of mycorrhizal hosts that germinate nearby are thereby inoculated (Maser et al. 1978). The obligatory relationship between mycorrhizal fungi and trees is traceable to the earliest known fossils of plant-rooting structures (Marks and Kozlowski 1973; Harley and Smith 1983). In an old-growth Douglas-fir stand in Oregon, the top 10 cm of soil was estimated to contain over 5000 kg/ha of mycorrhizae (Trappe and Fogel 1977). The enhanced dissemination of these symbionts by small mammals is an integral component of forest health.

3.4.2 Dispersal of seeds and other materials

Through their feeding activities, birds and mammals act as important dispersal agents of seeds. Such dispersal is important to maintain and spread woody plant populations, particularly in recently logged areas. It also promotes plant gene flow and population differentiation (van der Pijl 1972).

Most wildlife tree-dependent birds are insectivorous for at least part of the year (Tables 1–6) but only the ground-foraging guild is expected to disperse appreciable numbers of seeds.

Rodents (e.g., squirrels, chipmunks, mice) collect and store several kilograms of seeds annually (see references in Golley et al. 1975). By caching these seeds, they may satisfy the dormancy requirements for germination. They also consume seeds, some of which are adapted to pass through rodent digestive tracts unharmed. Digestive juices may weaken the seed coat, which favours water absorption and germination (Kreftig and Roe 1949). The digging and burrowing activities of various mammals expose mineral soil that provides a seedbed favouring seedling establishment.

Caches of seeds are deposited in areas of intense rodent activity where feces are abundant. As discussed above, these fecal pellets contain yeast and nitrogen-fixing bacteria in addition to mycorrhizal spores. The yeast stimulates growth and nitrogen fixation in the nitrogen-fixing bacteria (Li et al. 1986) and spore germination in the mycorrhizal fungi (Maser 1990). Transportation of seeds to areas where pellets are concentrated may therefore encourage establishment and early growth of seedlings (Maser 1990).

Small mammals accelerate organic decomposition through the cutting and transportation of leaves, stems, fungi and fruits which act as input to litter. Stark (1973) quantified the effect of squirrel feeding activity on the pine ecosystem as an increased litterfall of 18 g/m² per year. This effect could be important in nutrient-poor soils.

The physical and chemical properties of soils are improved by small mammals. Through their digging and burrowing activities, this guild mixes horizons of the soil profile. This increases nutrient availability in the soil, improves soil aeration, moisture-holding capacity and drainage from seepage areas (Spurr and Barnes 1980).

3.4.3 Provision of nesting, roosting and feeding opportunities

Primary cavity excavators play an important role in forest ecosystems by providing other cavity-dependent species with this critical habitat element (Beebe 1974b; Thomas et al. 1979). Nineteen species of birds in British Columbia are capable of excavating their own nest cavities. These include 12 woodpecker, 3 nuthatch and 4 chickadee species (Backhouse and Lousier 1991). Nuthatches and chickadees are classified as weak excavators and will occasionally nest in natural cavities or vacated

woodpecker cavities (Scott et al. 1977; Raphael and White 1984). Roosting cavities are also excavated by these species. Roosts provide resting, security and thermal cover, and winter roosts are considered critical for all of the nuthatches and chickadees and at least nine woodpecker species that are resident in the province (Cannings et al. 1987; Campbell et al. 1990).

There are 31 species of secondary cavity-using birds in British Columbia which depend on vacated or natural cavities for nesting (Backhouse and Lousier 1991). Some require cavities for roosting as well (Scott et al. 1977; Campbell et al. 1988). Beebe (1974b) reviewed studies that suggest scarcity of natural or vacated cavities, or, alternatively, suitable trees in which to excavate them, is the chief limiting factor for hole-nesting bird populations. Numerous examples of nest site competition and avian counter-adaptations to such competition are cited.

Twelve bat species in the province use natural or vacated cavities for hibernation, maternity colonies, maternal roosts and day or night roosts (Fitch and Shump 1979; Barclay 1985; Barclay et al. 1988; Backhouse and Lousier 1991). Hollow trees, tree crevices or openings under loose bark are occasionally used (van Zyll de Jong 1985; Nagorson and Brigham 1993). Suitable hibernacula and sites for maternity colonies and roosts may be the limiting factors for some bat species (Hill and Smith 1984; van Zyll de Jong 1985). Twelve rodent and seven carnivore species depend to some extent on vacated or natural tree cavities for nesting and denning in summer or winter (Backhouse and Lousier 1991). Primary cavity excavators provide a vital service to all these other wildlife tree-dependent groups, by excavating cavities directly and by loosening bark during their feeding activities.

Woodpeckers also provide other insectivores and herbivores with access to food resources. Some birds (e.g., Brown Creepers, Red-breasted Nuthatches) are attracted to woodpecker feeding excavations, where they feed on beetle broods, ants or exposed grubs (Kroll and Fleet 1979; Otvos 1979). Similarly, Hairy and Downy Woodpeckers are attracted to excavations made by Pileated Woodpeckers because they can forage more deeply than they could by their own efforts (Lawrence 1967; Maxson and Maxson 1981). Sapsuckers create sap wells in the bark of coniferous and deciduous trees

and shrubs (Tate 1973). Sap is an important seasonal component in the diet of these birds (Table 3; see also Tate 1973; Jackman 1975) and the use of sap wells by other birds (e.g., Williamson, Downy, Hairy and Three-toed Woodpeckers, White-breasted Nuthatch, House Wren, Mountain Chickadee, Ruby-crowned Kinglet, Yellow-rumped Warbler, Pine Siskin, American Goldfinch, Rufous and Broad-tailed Hummingbirds), mammals (e.g., chipmunks, squirrels) and insects (e.g., wasps, bees) is well documented (Batts 1953; Kilham 1953, 1958; Foster and Tate 1966; Jackman 1975; Miller and Nero 1983; Ehrlich and Daily 1988). The heavy use of late-summer sap wells by some groups (e.g., warblers, hummingbirds) suggests that this food resource could provide a dietary supplement during times of declining insect and floral nectar availability (Miller and Nero 1983; Ehrlich and Daily 1988). Sapsuckers can therefore be considered as “keystone herbivores” (Ehrlich and Daily 1988) by supplying other groups with access to a rich food source.

3.4.4 Accelerating decomposition in dead and decaying trees

Woodpeckers prefer to excavate nesting and roosting cavities in dead or decaying trees softened by fungal heart rots (Shigo and Kilham 1968; Kilham 1971; Conner et al. 1976; Bull and Meslow 1977; McClelland 1977; Mannon et al. 1980; Harestad and Keisker 1989; Bull et al. 1992). Such trees reduce the energetic requirements of cavity excavation, while maintaining a tough outer protective shell. Similarly, dead and decaying wood is a preferred foraging substrate for woodpeckers, probably because it harbours an abundance of bark-dwelling insects (Connor and Crawford 1974; Bull and Meslow 1977; Mannon et al. 1980; Raphael and White 1984; Bull 1987; Steeger et al. 1993). While feeding and excavating nest and roost cavities, woodpeckers provide secondary sites for insect attack and fungal infection. Ultimately, they accelerate the rate of tree decomposition and nutrient cycling in forest ecosystems (Otvos 1979).

3.4.5 Nutrient cycling

Because of their numbers and daily movements, bats may significantly enhance the nutrient status of regularly occupied roost trees, and on a larger scale, of entire forest ecosystems by depositing nitrogen-rich guano (Hutchinson 1950; Kunz 1982).

In temperate old-growth redwood forests, bats contribute an estimated 10–100 g/tree per year of guano which contain 10% N, compared to a background of 2–3 g of N/m² per year (Rainey et al. 1992). Values for guano deposition in provincial forests are not available now, but nutrient input by bats is expected to be significant (R. Barclay, University of Calgary, pers. comm., February 1993).

Birds and bats are probably more effective than any other group in transferring nutrients (e.g., calcium, nitrogen, phosphorus, sulfur, potassium, sodium, magnesium) within and between forest ecosystems because of their relative mobility (Sturges et al. 1974; DeGraaf 1977). Estimates of annual nutrient loss for birds are given in Sturges et al. (1974), with migratory species accounting for up to 16% of all phosphorus lost. At least 34 of the province's 58 (i.e., 59%) wildlife tree-dependent birds are resident species so nutrient loss attributed to this group is probably much less.

3.4.6 Vectors for the transmission of tree pathogens

Forest birds and mammals are implicated in the spread of tree diseases, both directly and indirectly (Otvos 1979; Ostry et al. 1982). Warner and French (1970) demonstrated that Common Grackles could transfer rust spores (*Puccinia* sp.) from infected to healthy seedlings. These spores remained viable and were recovered from the plumage up to 45 days after application. Similarly, forest birds (e.g., Mountain Chickadee) and mammals (e.g., Least Chipmunk) may accelerate the spread of dwarf mistletoe by transporting the seeds on their plumage or fur, and depositing them at uninfected sites (Zilka and Tinnin 1976; Ostry and Nicholls 1979; Hudler et al. 1979; Nicholls et al. 1986). Ostry et al. (1982) suggested that Downy Woodpeckers play a role in the spread of *Hypoxylon* sp. fungus, either by carrying fungal spores directly or by creating favourable conditions (through their feeding activity) for infection by airborne spores. Unidentified fungi invaded the galleries of southern pine beetle through openings created by woodpecker foraging (Dahlsten 1982). The extent of such transmission and its effect on forest health require further investigation.

3.4.7 Seed predation

Although seeds are included in the diet of 14 wildlife tree-dependent birds (Tables 3–6), they do not constitute the primary food for these species

(except for the House Finch). The most voracious avian seed predators in coniferous forests are not wildlife tree users (e.g., juncos, sparrows, towhees, thrushes; see references in Wiens 1975). Therefore, wildlife tree-dependent birds, as a group, are not expected to have a large impact on reforestation efforts.

Seeds are consumed by all terrestrial and arboreal rodents listed in Table 8 and some group members (e.g., *Peromyscus* sp., *Clethrionomys* sp., *Eutamias* sp.) are significant consumers of seeds during reforestation efforts (Radvanyi 1970; review in Pank 1974). An estimated five mice per hectare will remove 50 000 direct-seeded Douglas-fir seeds from a cutover area during a 15-day period (Sullivan 1978). Numerous techniques have been employed to control or eliminate seed-eating small mammal populations (e.g., slashburning, poison baiting, rodenticide-treated seeds, use of alternative foods, altering the timing of direct-seeding, etc.). These efforts have generally been unsuccessful (Sullivan 1979).

3.4.8 Damage to healthy trees

Woodpeckers tend to select dead or decaying trees for nest or roost cavity excavation. However, sound, live trees are occasionally used for nesting by Pileated Woodpeckers (McClelland 1979; Miller and Miller 1980; Harris 1983) and as foraging substrate by other woodpecker species (Conner and Crawford 1974; Mannon et al. 1980; Bull 1987). Some damage to isolated trees has been observed (Ziller and Stirling 1961); however, economic losses because of woodpecker activity are considered negligible (Finck et al. 1989).

Red Squirrels are considered the most important damage agents of juvenile lodgepole pine stands in the central Interior of British Columbia damaging up to 37% of the potential crop (Sullivan and Sullivan 1982; Sullivan and Vyse 1987). Squirrels strip bark from the stem and feed on the cambium and exposed sapwood. This can reduce the growth and vigour of a tree, increase its susceptibility to fungal attack or eventually kill the tree through girdling (Sullivan and Vyse 1987).

TABLE 1 Food habits of aquatic-foraging birds

| Species | Primary foods ^a | % A.F. ^b | General comments | Sources |
|--|--|---------------------|--|--|
| Wood Duck (<i>Aix sponsa</i>) | Aquatic plants, seeds and fruits of shrubs and trees, aquatic and terrestrial insects, other invertebrates | 13 | Insects increase to 16–27% of the diet in spring and summer | Martin et al. 1951; Ehrlich et al. 1988 |
| Common Goldeneye (<i>Bucephala clangula</i>) | Crustaceans, aquatic insects, molluscs, fish, aquatic vegetation | 74–85 | Aquatic insects make up 28% of the annual diet | Cottam 1939; Martin et al. 1951; Ehrlich et al. 1988 |
| Barrows Goldeneye (<i>Bucephala islandica</i>) | Aquatic insects, molluscs, crustaceans, aquatic vegetation | 78–85 | Aquatic insects make up 36% of the annual diet | Cottam 1939; Martin et al. 1951; Campbell et al. 1988; Ehrlich et al. 1988 |
| Bufflehead (<i>Bucephala albeola</i>) | Aquatic insects, crustaceans, molluscs, seeds of aquatic vegetation, fish | 75–80 | Aquatic insects make up 70% of the annual diet in freshwater | Martin et al. 1951; Erskine 1971; Scott et al. 1977; Ehrlich et al. 1988 |
| Hooded Merganser (<i>Lophodytes cucullates</i>) | Fish, crustaceans, aquatic insects, molluscs, frogs and tadpoles, snails | >90 | Aquatic insects make up 13% of the annual diet | Palmer 1976; Scott et al. 1977; Ehrlich et al. 1988 |
| Common Merganser (<i>Mergus merganser</i>) | Fish, crustaceans | >90 | — | Palmer 1976; Ehrlich et al. 1988 |
| Great Blue Heron (<i>Ardea herodias</i>) | Primarily fish; occasionally small mammals, reptiles, amphibians, birds, invertebrates, aquatic vegetation | — | — | Campbell et al. 1988; Ehrlich et al. 1988 |
| Osprey (<i>Pandion haliaetus</i>) | Primarily fish | 100 | — | Beebe 1974a; Machmer and Ydenberg 1990; Steeger et al. 1992 |
| Belted Kingfisher (<i>Ceryle alcyon</i>) | Primarily fish; occasionally aquatic invertebrates, reptiles, amphibians, insects | 100 | — | Ehrlich et al. 1988 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten “occasionally” when only qualitative data were available.

^b % A.F. = estimated percent of the diet volume consisting of food of animal origin.

TABLE 2 *Food habits of terrestrial-foraging raptors*

| Species | Primary foods ^a | % A. F. ^b | General comments | Sources |
|--|--|----------------------|---|---|
| Turkey Vulture (<i>Cathartes aura</i>) | Primarily carrion | >95 | — | Beebe 1974a; Ehrlich et al. 1988 |
| Bald Eagle (<i>Haliaeetus leucocephalus</i>) | Fish, small- to medium-sized birds, small mammals, carrion | 100 | Gallinaceous birds, waterfowl, seabirds | Beebe 1974a; Fielder 1982b; Stalmaster and Gessaman 1984; Ehrlich et al. 1988 |
| Northern Goshawk (<i>Accipiter gentilis</i>) | Small- to medium-sized birds, small mammals, lagomorphs, weasels | 100 | Gallinaceous birds, passerines waterfowl | Beebe 1974a; Campbell et al. 1988; Ehrlich et al. 1988 |
| Red-tailed Hawk (<i>Buteo jamaicensis</i>) | Small- to medium-sized mammals and birds; occasionally reptiles, amphibians and insects | 100 | Pocket gophers, ground squirrels weasels, lagomorphs | Beebe 1974a; Bruce et al. 1982; Ehrlich et al. 1988 |
| Golden Eagle (<i>Aquila chrysaetos</i>) | Medium-sized mammals, medium-sized birds; occasionally carrion | 100 | Marmots, lagomorphs; grouse, ptarmigan, pheasant | Beebe 1974a; Marr and Knight 1983; Ehrlich et al. 1988 |
| American Kestrel (<i>Falco sparverius</i>) | Small mammals; wide variety of large insects and small birds; occasionally reptiles and bats | 100 | Voles, mice, pocket gophers, chipmunks, ground squirrels | Beebe 1974a; Campbell et al. 1988; Ehrlich et al. 1988 |
| Merlin (<i>Falco columbarius</i>) | Primarily birds; occasionally insects and small mammals | 100 | >80% birds by biomass | Beebe 1974a; Scott et al. 1977; Ehrlich et al. 1988 |
| Barn Owl (<i>Tyto alba</i>) | Primarily small mammals; occasionally birds | 100 | Voles, mice, shrews, pocket gophers | Fielder 1982a; Taylor 1984; Bull and Akenson 1985; Campbell et al. 1988; Ehrlich et al. 1988 |
| Western Screech-Owl (<i>Otus kennicottii</i>) | Small mammals, arthropods, amphibians, reptiles, fish | 100 | Generalist; diet varies regionally | Marks and Marks 1981; Ehrlich et al. 1988 |
| Great Horned Owl (<i>Bubo virginianus</i>) | Lagomorphs, rodents, birds | 100 | Rabbit, snowshoe hare, pika; grouse, pheasants, waterfowl, passerines | Ehrlich et al. 1988 |
| Northern Hawk Owl (<i>Surnia ulula</i>) | Primarily small mammals; occasionally insects and birds | 100 | Voles, mice, shrews, lemmings | Bent 1961b; Ehrlich et al. 1988 |

TABLE 2 (Continued)

| Species | Primary foods ^a | % A.F. ^b | General comments | Sources |
|---|---|---------------------|--|---|
| Northern Pygmy-Owl (<i>Glaucidium gnoma</i>) | Primarily small mammals and small birds; occasionally reptiles, amphibians, large insects | 100 | Voles, mice; finches, sparrows, starlings, thrushes | Bent 1961b; Ehrlich et al. 1988 |
| Spotted Owl (<i>Strix occidentalis</i>) | Primarily rodents and lagomorphs; occasionally birds, reptiles and insects | 100 | Mice, rats, chipmunks, squirrels; >90% mammals by biomass | Bent 1961b; Forsman 1976; Ehrlich et al. 1988 |
| Barred Owl (<i>Strix varia</i>) | Small- to medium-sized mammals; some birds, reptiles and amphibians | 100 | Mice, voles, shrews, chipmunks, squirrels, lagomorphs, weasels | Bent 1961b; Marks et al. 1984; Campbell et al. 1988; Ehrlich et al. 1988 |
| Boreal Owl (<i>Aegolius funereus</i>) | Primarily small mammals and birds | 100 | Chipmunks, squirrels | Ehrlich et al. 1988 |
| Northern Saw-whet Owl (<i>Aegolius acadicus</i>) | Primarily small mammals; occasionally birds | 100 | Mice, voles, gophers; >95% small mammals in winter by biomass | Boula 1982; Grove 1985; Campbell et al. 1988; Ehrlich et al. 1988 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten "occasionally" when only qualitative data were available.

^b % A.F. = estimated percent of the diet volume consisting of food of animal origin.

TABLE 3 Food habits of bark-foraging birds

| Species | Primary foods ^a | % A.F. ^b | Major insect orders eaten | General comments | Sources |
|---|---|---------------------|--|---|---|
| Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>) | Insects, sap, bast, cambium, fruit | 50 | Hymenoptera, Coleoptera, Lepidoptera | Most insects taken in spring and summer; eats spruce budworms, tent caterpillars, sawflies | Beal 1911; Bent 1964c; Lawrence 1967; Tate 1973 |
| Red-naped Sapsucker (<i>Sphyrapicus nuchalis</i>) | Insects, sap, bast, cambium, fruit, spiders | 50 | Coleoptera, Hymenoptera, Orthoptera | Most insects taken in spring and summer | Beal 1911; Bent 1964c; Ehrlich et al. 1988 |
| Red-breasted Sapsucker (<i>Sphyrapicus ruber</i>) | Insects, sap, bast, cambium, fruit | 53–69 | Hymenoptera, Coleoptera, Homoptera, Trichoptera, Lepidoptera | Most insects taken in spring and summer | Beal 1911; Bent 1964c; Jackman 1975; Otvos and Stark 1985; Ehrlich et al. 1988 |
| Williamson Sapsucker (<i>Sphyrapicus thyroideus</i>) | Insects; occasionally cambium, sap | 87–92 | Hymenoptera, Coleoptera | Ants comprise most of diet; eats bark beetles | Beal 1911; Bent 1964c; Otvos and Stark 1985 |
| Downy Woodpecker (<i>Picoides pubescens</i>) | Insects; occasionally sap, fruits, cambium, seeds | 76–97 | Coleoptera, Hymenoptera, Lepidoptera | Beetles make up >40% of diet volume; two-thirds are wood-boring buprestids, cerambycids and scolytids; eats larch and pine sawflies, codling moth | Beal 1911; Bent 1964c; Otvos and Stark 1985 |
| Hairy Woodpecker (<i>Picoides villosus</i>) | Insects; occasionally fruits, seeds | 77–93 | Coleoptera, Hymenoptera | Beetles make up >60% of diet volume; most beetles are wood-boring buprestids, cerambycids and scolytids; eats larch sawfly, codling moth | Beal 1911; Bent 1964c; Otvos and Stark 1985; Villard and Beninger 1993 |
| White-headed Woodpecker (<i>Picoides albolarvatus</i>) | Insects, pine cones, spiders | 40–80 | Coleoptera, Hymenoptera, Homoptera | Most cones taken in spring, insects in summer, cones and insects in fall/winter; eats bark beetles | Beal 1911; Bent 1964c; Ligon 1973 |
| Three-toed Woodpecker (<i>Picoides tridactylus</i>) | Insects | 89–96 | Coleoptera, Lepidoptera | >75% of diet volume consists of wood-boring beetles; eats larch sawfly | Beal 1911; Stallcup 1962; Bent 1964c; Otvos and Stark 1985; Goggins et al. 1989 |

TABLE 3 (Continued)

| Species | Primary foods ^a | % A.F. ^b | Major insect orders eaten | General comments | Sources |
|--|--|---------------------|---|---|--|
| Black-backed Woodpecker (<i>Picooides articus</i>) | Insects; occasionally fruit, mast, cambium | >90 | Coleoptera, Hymenoptera | >75% of diet volume consists of wood-boring beetles; consume ~13,675 beetle larvae per bird annually | Bent 1964c; Goggins et al. 1989; Villard and Beninger 1993 |
| Northern Flicker (<i>Colaptes auratus</i>) | Insects; occasionally nuts, grains and fruits | 61–95 | Hymenoptera, Coleoptera, Orthoptera, Lepidoptera | Strong seasonal diet trends; ants comprise ~75% of insect food by volume | Beal 1911; Martin et al. 1951; Bent 1964c; Otvos and Stark 1985; Campbell et al. 1988 |
| Pileated Woodpecker (<i>Dryocopus pileatus</i>) | Insects; occasionally fruits and nuts | 73–75 | Hymenoptera, Coleoptera, Lepidoptera | Ants (<i>Camponotus</i> sp.) comprise >50% of diet volume; eats bark beetles and spruce budworms | Beal 1911; Bent 1964c; Beckworth and Bull 1985; Otvos and Stark 1985; Bull et al. 1992 |
| Red-breasted Nuthatch (<i>Sitta canadensis</i>) | Insects; occasionally seeds and spiders | 70–88 | Coleoptera, Hymenoptera, Hemiptera, Dermoptera | Diet includes bark-dwelling forms such as bark beetles, weevils, wood-borers; eats spruce and jack pine budworm, Douglas-fir tussock moth | Bent 1964b; Stallcup 1963; Anderson 1976; Campbell et al. 1988 |
| White-breasted Nuthatch (<i>Sitta carolinensis</i>) | Insects; occasionally spiders, seeds and nuts | 83–92 | Coleoptera, Hymenoptera, Lepidoptera, Dermoptera, Hemiptera | Diet includes bark-dwelling forms such as bark beetles, weevils, wood-borers; eats gypsy moths, tent caterpillars, spruce budworm | Bent 1964b; Stallcup 1963; Anderson 1976 |
| Pygmy Nuthatch (<i>Sitta pygmaea</i>) | Insects; also conifer seeds and spiders | 83 | Coleoptera, Hymenoptera, Hemiptera, Lepidoptera | Diet includes several bark beetles, wood-boring beetles, leaf bugs and weevils; eats spruce budworm | Stallcup 1963; Bent 1964b; Anderson 1976; Otvos and Stark 1985 |
| Brown Creeper (<i>Certhia americana</i>) | Insects and spiders; occasionally nuts and seeds | >85 | Lepidoptera, Diptera, Coleoptera, Hemiptera, Homoptera | Diet includes many injurious forms such as bark beetles, wood-borers, larch sawfly, spruce budworm | Beal 1911; Stallcup 1963; Otvos and Stark 1985; Mariani and Manuwal 1990 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten “occasionally” when only qualitative data were available.

^b % A.F. = estimated percent of the diet volume consisting of food of animal origin.

TABLE 4 Food habits of foliage-gleaning birds

| Species | Primary foods ^a | % A.F. ^b | Major insect orders eaten | General comments | Sources |
|---|--|---------------------|--|---|--|
| Black-capped Chickadee (<i>Parus atricapillus</i>) | Insects; occasionally seeds, fruit and spiders | 70 | Lepidoptera, Coleoptera, Hemiptera, Hymenoptera | Eats codling and gypsy moth, spruce and jack pine budworm, larch and pine sawfly, larch casebearer, Douglas-fir tussock moth, forest loopers, wood-borers, bark beetles and weevils | Martin et al. 1951; Bent 1964a; Scott et al. 1977 |
| Mountain Chickadee (<i>Parus gambeli</i>) | Insects; occasionally seeds, nuts, berries and spiders | 75-98 | Hymenoptera, Lepidoptera, Coleoptera, Diptera, Homoptera | Eats spruce budworm, Douglas-fir tussock moth, sawflies, spruce aphids, needle miners, forest loopers, injurious geometrids and tortricids and bark beetles | Scott et al. 1977; Dahlsten and Copper 1979; Campbell et al. 1988; Grundel and Dahlsten 1991 |
| Boreal Chickadee (<i>Parus hudsonicus</i>) | Insects; occasionally seeds, berries and spiders | — | Lepidoptera, Homoptera, Coleoptera | Eats spruce and black-headed budworm, larch sawfly, forest loopers and bark beetles | Bent 1964a; Scott et al. 1977; Campbell et al. 1988 |
| Chestnut-backed Chickadee (<i>Parus rufescens</i>) | Insects; occasionally seeds, fruits and spiders | 65 | Lepidoptera, Hemiptera, Homoptera, Coleoptera | Eats spruce budworm, Douglas-fir tussock moth, forest loopers, sawflies and bark beetles | Bent 1964a; Scott et al. 1977 |

^a Primary foods = foods that make up ≥ 10% of the diet volume in any season or foods eaten “occasionally” when only qualitative data were available.

^b % A.F. = estimated percent of the diet volume consisting of food of animal origin.

TABLE 5 Food habits of aerial-foraging and hawking birds

| Species | Primary foods ^a | % A.F. ^b | Major insect orders eaten | General comments | Sources |
|---|---|---------------------|--|---|---|
| Flammulated Owl (<i>Otus flammeolus</i>) | Insects; some spiders, birds and mammals | 100 | Lepidoptera, Coleoptera, Orthoptera | — | Bull and Anderson 1978; Campbell et al. 1988; Ehrlich et al. 1988 |
| Lewis Woodpecker (<i>Melanerpes lewis</i>) | Insects, fruit, nuts, berries, seeds, spiders | 37 | Coleoptera, Hymenoptera, Orthoptera, Hemiptera, Diptera | Most insects eaten in summer; eats adult emergent insects (no wood-boring larvae); eats tent caterpillars | Beal 1911; Bent 1964c; Bock 1970; Jackman 1975 |
| Vaux's Swift (<i>Chaetura vauxi</i>) | Insects | 100 | Diptera, Coleoptera, Hymenoptera, Hemiptera | Eats exclusively flying insects | Martin et al. 1951; Scott et al. 1977 |
| Pacific-slope Flycatcher (<i>Empidonax difficilis</i>) | Insects | 100 | Hymenoptera, Diptera, Hemiptera, Coleoptera, Lepidoptera | Eats bark beetles | Martin et al. 1951; Bent 1963; Stallcup 1963; Scott et al. 1977 |
| Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>) | Insects; occasionally spiders, fruits and berries | 92 | Hymenoptera, Hemiptera, Coleoptera, Lepidoptera, Diptera | — | Bent 1963; Scott et al. 1977, Otvos and Stark 1985 |
| Purple Martin (<i>Progne subis</i>) | Insects; occasionally spiders | 100 | Hymenoptera, Diptera, Hemiptera, Coleoptera, Lepidoptera, Odonata | — | Bent 1963; Scott et al. 1977, Walsh 1978; Otvos and Stark 1985 |
| Tree Swallow (<i>Tachycineta bicolor</i>) | Insects; occasionally spiders, seeds and berries | 80 | Coleoptera, Hymenoptera, Odonata, Ephemeroptera, Orthoptera | Eats larch sawfly and bark beetles | Bent 1963; Campbell et al. 1988 |
| Violet-green Swallow (<i>Tachycineta thalassina</i>) | Insects | 100 | Hemiptera, Diptera, Hymenoptera, Coleoptera, Lepidoptera | Preys on several injurious insects including scolytids and engraver beetles | Bent 1963; Otvos and Stark 1985 |
| Western Bluebird (<i>Sialia mexicana</i>) | Insects; occasionally spiders and fruits | 80 | Coleoptera, Hymenoptera, Hemiptera, Lepidoptera, Orthoptera | — | Bent 1964d; Herlugson 1982 |
| Mountain Bluebird (<i>Sialia currucoides</i>) | Insects; occasionally fruits and spiders | 90 | Coleoptera, Hymenoptera, Lepidoptera, Hemiptera, Orthoptera, Homoptera | Eats bark beetles | Stallcup 1963; Bent 1964d; Power 1980; Herlugson 1982 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten "occasionally" when only qualitative data were available.

^b % A.F. = estimated percent of the diet volume consisting of food of animal origin.

TABLE 6 Food habits of ground-foraging birds

| Species | Primary foods ^a | % A.F. ^b | Major insect orders eaten | General comments | Sources |
|---|--|---------------------|---|---|--|
| Bewick's Wren (<i>Thryomanes bewickii</i>) | Insects | 97 | Hemiptera, Coleoptera, Orthoptera | Eats injurious forms (e.g., weevils, bark beetles, locusts) | Bent 1964b; Ehrlich et al. 1988 |
| House Wren (<i>Troglodytes aedon</i>) | Insects; also spiders, snails and millipedes | 98 | Hemiptera, Lepidoptera, Coleoptera, Hymenoptera, Orthoptera | Eats bark beetles | Bent 1964b; Scott et al. 1977; Ehrlich et al. 1988 |
| Common Grackle (<i>Quiscalus quiscula</i>) | Insects, spiders, crustaceans, earthworms, snails, birds' eggs, small vertebrates, fruit, grain, seeds and nuts | 32 | Hymenoptera, Orthoptera | Omnivorous; eats spruce and jackpine budworm | Martin et al. 1951; Ehrlich et al. 1988 |
| House Finch (<i>Carpodacus mexicanus</i>) | Seeds, fruits, buds and tree sap | — | — | — | Ehrlich et al. 1988 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten "occasionally" when only qualitative data were available.

^b % A.F. = estimated percent of the diet volume consisting of food of animal origin.

TABLE 7 Food habits of aerial-foraging and gleaning bats

| Species | Primary foods ^a | Major insect orders eaten | General comments | Sources |
|---|--|---|--|--|
| Pallid Bat (<i>Antrozous pallidus</i>) | Insects, spiders, small vertebrates | Coleoptera, Lepidoptera, Orthoptera | Prefers insects >17 mm; prey includes flightless forms gleaned from the ground or foliage | Easterla and Whitaker 1972; Whitaker et al. 1977; Bell 1982; Nagorson and Brigham 1993 |
| Big Brown Bat (<i>Eptesicus fuscus</i>) | Insects | Coleoptera, Lepidoptera, Diptera, Isoptera, Hemiptera | Prefers insects 6–12 mm; prey includes flightless forms such as beetle larvae and spiders | Whitaker et al. 1977, 1981a; Brigham 1990; Brigham and Saunders 1990; Nagorson and Brigham 1993 |
| Silver-haired Bat (<i>Lasionycteris noctivagans</i>) | Insects | Lepidoptera, Homoptera, Hymenoptera, Diptera, Coleoptera, Isoptera | Diet is extremely flexible | Whitaker et al. 1977, 1981a, 1981b; Nagorson and Brigham 1993 |
| Hoary Bat (<i>Lasiurus cinereus</i>) | Insects | Lepidoptera, Coleoptera, Diptera, Odonata | Prey size range: 6–30 mm | Whitaker et al. 1977, 1981a; Barclay 1985; Nagorson and Brigham 1993 |
| California Myotis (<i>Myotis californicus</i>) | Insects; occasionally spiders | Lepidoptera, Trichoptera, Diptera, Coleoptera | Prey includes flightless forms gleaned from the ground or foliage | Whitaker et al. 1977, 1981b; Nagorson and Brigham 1993 |
| Western Small-footed Myotis (<i>Myotis ciliolabrum</i>) | Insects | Trichoptera, Diptera, Lepidoptera, Coleoptera, Hemiptera | — | Whitaker et al. 1981b; Woodsworth 1981; Nagorson and Brigham 1993 |
| Western Long-eared Myotis (<i>Myotis evotis</i>) | Insects; occasionally spiders | Lepidoptera, Coleoptera, Diptera | Preys on many flightless forms | Whitaker et al. 1977, 1981a; Faure and Barclay 1992; Nagorson and Brigham 1993 |
| Keen's Long-eared Myotis (<i>Myotis keenii</i>) | Insects | Lepidoptera | Very little information available on diet | Van Zyll de Jong 1985; Nagorson and Brigham 1993 |
| Little Brown Myotis (<i>Myotis lucifugus</i>) | Insects | Diptera, Lepidoptera, Coleoptera, Trichoptera | Prefers insects 6–10 mm | Whitaker et al. 1977, 1981a; Herd and Fenton 1983; Nagorson and Brigham 1993 |
| Northern Long-eared Myotis (<i>Myotis septentrionalis</i>) | Insects | Trichoptera, Lepidoptera, Coleoptera, Diptera, Homoptera, Hymenoptera | — | Whitaker 1972; Nagorson and Brigham 1993 |

TABLE 7 (Continued)

| Species | Primary foods ^a | Major insect orders eaten | General comments | Sources |
|--|----------------------------|--|---------------------------------|--|
| Long-legged Myotis (<i>Myotis volans</i>) | Insects | Lepidoptera, Hymenoptera, Diptera, Coleoptera, Homoptera | — | Black 1974; Whitaker et al. 1977, 1981a; Nagorson and Brigham 1993 |
| Yuma Myotis (<i>Myotis yumanensis</i>) | Insects | Ephemeroptera, Trichoptera, Diptera, Lepidoptera, Coleoptera, Isoptera, Homoptera | Feeds mainly on aquatic insects | Easterla and Whitaker 1972; Whitaker et al. 1977, 1981a; Brigham et al. 1992; Nagorson and Brigham 1993 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten "occasionally" when only qualitative data were available.

TABLE 8 Food habits of terrestrial and arboreal rodents

| Species | Primary foods ^a | General comments | Sources |
|--|--|---|--|
| Southern Red-backed Vole (<i>Clethrionomys gapperi</i>) | Fungi, lichens, seeds, berries, shoots and petioles of graminoids, forbs and shrubs, insects | 72% fungi in the diet by volume; eats larch sawfly | Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978; Gunther et al. 1983; Stevens and Lofts 1988 |
| Bushy-tailed Wood Rat (<i>Neotoma cinerea</i>) | Green and dry foliage of forbs, shrubs and trees; fungi, lichens, fruits and seeds; occasionally insects and carrion | 34% fungi in the diet by volume | Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978; Stevens and Lofts 1988 |
| Deer Mouse (<i>Peromyscus maniculatus</i>) | Arthropods, seeds, fruits, fungi, lichens, stems and roots of grasses | 46% animal food and 10% fungi in the diet by volume (e.g., Coleoptera, Lepidoptera, Diptera); eats gypsy moth and pine sawfly | Martin et al. 1951; Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978; Gunther et al. 1983; Stevens and Lofts 1988 |
| Columbian Mouse (<i>Peromyscus ureas</i>) | Arthropods, seeds, fruits, fungi, lichens, stems and roots of grasses | No information on fungus consumption | Cowan and Guiget 1978 |
| Sitka Mouse (<i>Peromyscus sitkensis</i>) | — | No specific dietary information available | — |
| Northern Flying Squirrel (<i>Glaucomys sabrinus</i>) | Primarily fungi and lichens; occasionally buds, fruits, seeds, shrubs, mosses, forbs and insects | 78% fungi in the diet by volume; insect orders consumed include Lepidoptera and Coleoptera | Martin et al. 1951; McKeever 1960; Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978; Stevens and Lofts 1988 |
| Yellow-pine Chipmunk (<i>Tamias amoenus</i>) | Fungi, seeds, flowers, fruits, bulbs, tubers and insects | 50% fungi in the diet by volume | Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978; Maser and Maser 1987; Stevens and Lofts 1988 |
| Least Chipmunk (<i>Tamias minimus</i>) | Seeds, fruits, fungi and insects | No information on fungus consumption; eats jack pine budworm | Martin et al. 1951; Cowan and Guiget 1978; Fogel and Trappe 1978 |

TABLE 8 (Continued)

| Species | Primary foods ^a | General comments | Sources |
|---|--|--|---|
| Red-tailed Chipmunk (<i>Tamias ruficaudus</i>) | — | No specific dietary information available | — |
| Townsend's Chipmunk (<i>Tamias townsendii</i>) | Primarily fungi; occasionally berries, seeds and nuts | 77% fungi in the diet by volume | Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978 |
| Douglas Squirrel (<i>Tamiasciurus douglasii</i>) | Fungi, conifer seeds, fruits, buds, insects, sap, cambium | 70% fungi in the diet by volume | Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978 |
| Red Squirrel (<i>Tamiasciurus hudsonicus</i>) | Primarily fungi; also seeds, nuts, lichens, fruits, buds, insects, small vertebrates, sap, cambium | 77% fungi in the diet by volume; eats jack pine budworm and spruce budworm | Cowan and Guiget 1978; Fogel and Trappe 1978; Maser et al. 1978; Stevens and Lofts 1988 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten "occasionally" when only qualitative data were available.

TABLE 9 Food habits of carnivores

| Species | Primary food ^a | General comments | Sources |
|--|--|--------------------------------------|---|
| Marten (<i>Martes americana</i>) | Rodents, lagomorphs; occasionally birds, fish, vegetation, insects and crustaceans | Voles, mice and squirrels | Stordeur 1986; Stevens and Lofts 1988 |
| Fisher (<i>Martes pennanti</i>) | Lagomorphs, porcupine, rodents, birds, carrion, insects, fruit and berries | Squirrels, voles, mice and shrews | Cowan and Guiget 1978; Powell 1982; Stevens and Lofts 1988 |
| Ermine (<i>Mustela erminea</i>) | Small mammals, birds, fish, amphibians and insects; some vegetation | Voles, squirrels, chipmunks and mice | Stordeur 1986; Stevens and Lofts 1988; Nagorson et al. 1989 |
| Long-tailed Weasel (<i>Mustela frenata</i>) | Small mammals, pikas; occasionally birds | Voles, mice and squirrels | Cowan and Guiget 1978; Stevens and Lofts 1988 |
| Least Weasel (<i>Mustela nivalis</i>) | Primarily microtine rodents; occasionally small birds, amphibians and reptiles | — | Cowan and Guiget 1978 |
| Spotted Skunk (<i>Spilogale putorius</i>) | Mice, birds, amphibians, reptiles, insects, fungi; occasionally fruit | — | Fogel and Trappe 1978; Cowan and Guiget 1978 |
| Raccoon (<i>Procyon lotor</i>) | Arthropods, birds, small mammals, fish, frogs, berries, fruits, nuts, seeds and eggs | Omnivorous | Cowan and Guiget 1978; Stevens and Lofts 1988 |
| Black Bear (<i>Ursus americanus</i>) | Leaves, shoots, buds, sapwood, fruits, fungi, insects, fish, carrion, small- to medium-sized mammals and ungulates | Omnivorous | Cowan and Guiget 1978; Stevens and Lofts 1988 |

^a Primary foods = foods that make up $\geq 10\%$ of the diet volume in any season or foods eaten “occasionally” when only qualitative data were available.

TABLE 10 Summary of quantitative studies of avian predation on forest pests

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/conclusions |
|--|---|---------------------------|-------------------------|--|-----------------------------|------------------------|---|
| <u>Order Coleoptera</u> | | | | | | | |
| Woodpecker guild (TTWO, HAWO, DOWO) | Engelmann spruce beetle (<i>Dendroctonus engelmannii</i>) | EPI | L | 99% of woodpecker diet in winter consisted of spruce beetle larvae | 55% | Hutchinson 1951 | Mortality estimated for 3 species. |
| Woodpecker guild (TTWO, HAWO, DOWO) | Engelmann spruce beetle | END | L | — | 45–98% | Knight 1958 | Mortality estimated for 3 species. Prey mortality depended on intensity of localized woodpecker activity; mortality per tree was highly correlated with % bark removed by woodpeckers. Conclude: 3 species are important in control of spruce beetle. |
| Woodpecker guild (TTWO, HAWO, DOWO) | Engelmann spruce beetle | EPI | L | — | 45–98% | Baldwin 1960 | Mortality estimated for 3 species; includes direct and indirect effects of woodpecker feeding activity. Strong numerical response by all 3 species (30-fold increase in woodpecker density during EPI). |
| Avian guild (incl. MOCH, MOBL, and 4 non-WT species) | Engelmann spruce beetle | END–TR | A | — | 24–32% | Baldwin 1968 | Mortality estimated for entire guild (6 species). Conclude: birds have an important impact on adult spruce beetles when prey at moderate densities. |
| Woodpecker guild (TTWO, HAWO) | Engelmann spruce beetle | END | L | — | 52–83% | Shook and Baldwin 1970 | Mortality estimated for both species. Prey mortality was influenced by stand density: semi-open = 83%; open = 71%; dense = 52%. Conclude: woodpeckers are important in controlling END spruce beetle populations. |

TABLE 10 (Continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|---|---|---------------------------|-------------------------|--|-----------------------------|-----------------------------------|---|
| Woodpecker guild (TTWO, HAWO, DOWO) | Engelmann spruce beetle | END | L | TTWO: 400 L/ha per yr HAWO: 50 L/ha per yr DOWO: 0 L/ha per yr | 19% | Koplin 1972 | Mortality estimated for 3 species; all 3 species: functional and numerical response to increased prey density. Combined predatory impact was greatest at EPI prey density. Decreased effect at END prey density because of availability of alternative prey; decreased impact at PAN prey density because of limits imposed by nesting territoriality on numerical response. From END to EPI prey density, 50–85-fold increase in woodpecker winter density and 6–7-fold increase in woodpecker breeding density. Conclude: woodpecker predation can limit EPI but not PAN spruce beetle infestations. |
| | | EPI | L | TTWO: 178 000 L/ha per yr HAWO: 110 000 L/ha per yr DOWO: 49 250 L/ha per yr | 83% | | |
| | | PAN | L | TTWO: 1 165 250 L/ha per yr HAWO: 535 750 L/ha per yr DOWO: 387 250 L/ha per yr | 55% | | |
| Woodpecker guild (TTWO, HAWO, DOWO) | Engelmann spruce beetle | END | L | TTWO: 42 L/predator stomach HAWO: 7 L/predator stomach | 20–29% | Koplin and Baldwin 1970 | Mortality estimated for 3 species; all 3 species: functional and numerical response to increased prey density. Spruce beetle larvae made up 2–7% and 4–29% of the items in woodpecker diet at END and EPI prey densities, respectively. Conclude: woodpeckers are important regulators of spruce beetle. |
| | | | L | TTWO: 915 L/predator stomach HAWO: 154 L/predator stomach DOWO: 45 L/predator stomach | 45–98% | | |
| Woodpecker guild (TTWO, HAWO, DOWO) | Spruce beetle (<i>Dendroctonus rufipennis</i>) | EPI | L | — | 24–98% | McCambridge and Knight 1972 | Mortality estimated for 3 species; includes direct and indirect effects (e.g., desiccation, changes in parasite and predator density) of woodpecker feeding activity. |

TABLE 10 (Continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|---|---|---------------------------|-------------------------|--|-----------------------------|---------------------------|---|
| Avian guild (incl. TTWO, HAWO, and non-WT species) | Mountain pine beetle (<i>Dendroctonus ponderosae</i>) | EPI | A | TTWO: 3–75 A/predator stomach HAWO: 2–14 A/predator stomach | — | Rust 1929, 1930 | Woodpeckers showed a numerical response to localized increases in mountain pine beetle density. |
| Avian guild (incl. RBNU, BRRCR, PYNU, and non-WT species) | Mountain pine beetle | EPI | A | guild: 2358 A/acre per season | 11.6% | Stallcup 1963 | Mortality estimated for entire guild (? species). Most important predators were RBNU, BRRCR, PYNU and <i>Empidonax</i> spp. flycatchers. Conclude: birds contribute to control during the flight and attack period of adult beetles. |
| Woodpecker guild (HAWO, DOWO) | Mountain pine beetle | END | L, A | — | 27–54% | Amman 1973 | Mortality estimated for both species. Woodpecker predation on adults increased with elevation; larvae are smaller and less preferred at higher elevations. |
| Woodpecker guild (TTWO, HAWO, DOWO) | Mountain pine beetle | EPI | L, A | Beetle adults and larvae made up 67–99% of the winter diet volume for all predator species | 45–95% | Crockett and Hansley 1978 | Mortality estimated for 3 species; estimates include direct and indirect effects (e.g., desiccation, freezing, changes in parasite and predator density) of woodpecker feeding activity. 2–3.5-fold increase in woodpecker density during outbreak. Secondary infection by other wood-borers increased intensity and duration of predator response. |
| Woodpecker guild (DOWO, HAWO, TTWO, BBWO, PIWO) | Mountain pine beetle | EPI | L, A | — | 30% — | Lester 1980 | Mortality estimated for 5 species. HAWO and TTWO: strong numerical response in EPI vs. END areas. Conclude: woodpeckers more important at END prey density. |

TABLE 10 (continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|--|--|---------------------------|-------------------------|--|---------------------------------------|----------------------------|---|
| Avian guild (HAWO, RBNU, BR CR) | Mountain pine beetle | END–EPI | L, A | HAWO: 21 108 L/ha per season (theoretical maximum) Guild: 329 A/ha per season | | Korol 1985 | Consumption is likely underestimated because only data on 3 species were adequate for inclusion in the model. Conclude: birds may suppress prey growth and maximum prey density; silvicultural methods and retention of wildlife trees could prevent growth of EPI from END prey densities. |
| Downy Woodpecker | Mountain pine beetle | EPI | L | — | 50–90% | Bergvinson and Borden 1992 | Herbicide-treated trees increased DOWO predation efficiency to 90% from 50% in control trees. Conclude: treating trees would enhance woodpecker nesting and feeding habitat and decrease beetle impact. |
| Woodpecker guild (HAWO, DOWO, WHWO, PIWO) | Western pine beetle (<i>Dendroctonus brevicomis</i>) | EPI | L, A | — | 31.8% | Otvos 1965 | Mortality estimated for entire guild; includes only direct impact of woodpecker feeding activity. Woodpecker activity increased beetle parasite densities 4-fold and decreased insect predation on beetles slightly. |
| Avian guild (incl. VGSW, RBNU, and 4 non-WT species) | Western pine beetle | EPI | A | — | 8–26% | Otvos 1969, 1970 | Mortality estimated for entire guild; range is over 3 years. Conclude: avian predation can contribute to control of adult beetle densities. |
| Downy Woodpecker | Southern pine beetle (<i>Dendroctonus frontalis</i>) | EPI | L | — | 7% in winter and spring; 2% in summer | Moore 1972 | Mortality estimate includes direct effect of woodpecker feeding only. Woodpecker feeding increased desiccation of inner bark and caused weather and disease to increase brood mortality; this effect was not quantified. |

TABLE 10 (Continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|---|---|---------------------------|-------------------------|-----------------------------------|--|---|---|
| Woodpecker guild (incl. DOWO, HAWO, PIWO) | Southern pine beetle | EPI | E, P, A | — | 3.5% E; 12–30% P, A in summer; 36–63% P, A in winter | Kroll and Fleet 1979; Kroll et al. 1980 | Mortality estimated for entire guild. Woodpecker density increased 6–33-fold in EPI vs. END prey areas. Conclude: woodpeckers play a role in stabilizing southern pine beetle population densities. |
| Woodpecker guild (TTWO, HAWO) | <i>Ips</i> beetle (several species) | END | — | — | 11–76 % | Shook and Baldwin 1970 | Mortality estimated for both species. Beetle mortality influenced by stand density: 76% = open; 11% = semi-open. Conclude: woodpeckers contribute to control of END beetle densities. |
| Black-backed Woodpecker | Oregon fir sawyer (<i>Monochamus oregonensis</i>) | EPI | L | BBWO: 10–12 L/day | 90% | Wickman 1965 | Conclude: BBWO feeding activity is an important source of pest control. |
| Woodpecker guild (incl. HAWO, DOWO, PIWO) | Hardwood borers (14 species) | EPI | L | — | 13–65 % | Solomon 1969 | Mortality estimated for entire guild. Woodpeckers preyed on 14 species of borers. Tree diameter at breast height was inversely related to woodpecker predation success. |
| Woodpecker guild (DOWO, HAWO) | Red oak borer (<i>Enaphalodes rufulus</i>) | END | L | — | 9.4% | Petit and Grubb 1988 | Mortality estimated for both species. Study conducted in clearcut where woodpecker densities were low, probably because of lack of nest sites. |
| Order Lepidoptera | | | | | | | |
| Avian guild (incl. BCCH) | Larch case- bearer (<i>Coleophora laricella</i>) | END | L | — | 23.5% | Sloan and Coppel 1968 | Mortality estimated for entire guild (? species). Conclude: predation by birds contributes to prey population stability. |

TABLE 10 (continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|---|--|---------------------------|-------------------------|--|-----------------------------|---|--|
| Mountain Chickadee | Lodgepole needle miner (<i>Coleotechnites starki</i>) | EPI | L | Larvae made up >90% of the stomach volume of overwintering MOCH | — | Telford and Herman 1963 Dahlsten and Herman 1965 | MOCH: functional and numerical response to increased prey density. |
| Mountain Chickadee | Douglas-fir tussock moth (<i>Orgyia pseudotsugata</i>) | END | L, P, E | — | 16.7% | Dahlsten and Copper 1979 | MOCH fed mainly on egg masses and cocoons. Predation rates were correlated with MOCH nest densities. Conclude: bird density may be important in moth suppression. |
| | | TR | L, P, E | — | 66.7% | | |
| | | EPI | L, P, E | — | 71.7% | | |
| Avian guild (incl. RBNU, MOCH, BCCH, CBCH, and 17 non-WT species) | Douglas-fir tussock moth | — | L, P | Used number of observed predation events as an indication of relative consumption: RBNU: 24 events MOCH: 4 events BCCH: 1 event CBCH: 2 events | 43% | Torgerson et al. 1984 | Mortality estimated for entire guild. MOCH and RBNU are the two most important predators based on their density and observed consumption. Loss rates of prey were positively associated with concurrent densities of avian predators. |
| Woodpecker guild (DOWO, HAWO) | Codling moth | EPI | L | — | HAWO: 34.8% DOWO: 17.2% | MacLellan 1958 | Only 3% of larvae eaten by woodpeckers were parasitized; 14% of escaped larvae were parasitized. Orchard density effected mortality by woodpecker predation: dense = 64%; semi-open = 49%; open = 35%. Conclude: both species important in control of moth larvae. |
| Avian guild (incl. BOCH) | Black-headed budworm (<i>Acleris variana</i>) | END | L, P | 15 prey/predator per day | 3–14% | Gage et al. 1970 | Mortality estimated for entire guild (? species). BOCH: positive functional and numerical response to increased prey density. |

TABLE 10 (continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/conclusions |
|---|--|---------------------------|-------------------------|--|-----------------------------|--------------------------|--|
| Avian guild (incl. BCCH, RBNU, COGR) | Jack pine budworm (<i>Choristoneura pinus</i>) | END | L, P | BCCH: 7 prey/predator stomach RBNU: 2 prey/predator stomach COGR: 43 prey/predator stomach | 40–65% | Mattson et al. 1968 | Mortality estimated for entire guild (? species). BCCH and RBNU: strong numerical response. Conclude: birds play a role in moth control at END prey density. |
| Avian guild (incl. BCCH) | Jack pine budworm | END | L, P | BCCH: 8.4 prey/predator stomach | — | Mattson 1975 | BCCH: no functional response observed from END to TR prey densities. Conclude: birds important at END prey density only. |
| | | TR | L, P | BCCH: 6.3 prey/predator stomach | | | |
| Avian guild (incl. BCCH) | Eastern spruce budworm (<i>Choristoneura fumiferana</i>) | EPI | L | 40 L/predator per day | 4.3% | Kendeigh 1947 | Mortality estimated for entire guild (? species). |
| Avian guild (incl. chickadees, nuthatches, creepers) | Eastern spruce budworm | EPI | L | 65–100 L/predator per day | 3.5–7% | George and Mitchell 1948 | Mortality estimated for entire guild (? species). Conclude: birds more important at END prey densities. |
| Avian guild (incl. BCCH, RBNU, COGR, and 12 other non-WT species) | Eastern spruce budworm | END | L, P | BCCH: 2.9 prey/day per ha RBNU: 3.6 prey/day per ha | 87% | Crawford et al. 1983 | Mortality estimated for entire guild (15 species). BCCH and RBNU increased consumption rates from END to TR prey densities; no increased consumption rates from TR to EPI prey densities. Conclude: some species (e.g., BCCH, RBNU) are important in pest suppression and may prevent or reduce the severity of budworm outbreaks. |
| | | TR | L, P | BCCH: 17 prey/day per ha RBNU: 30 prey/day per ha | 23% | | |
| | | EPI | L, P | BCCH: 122 prey/day per ha RBNU: 124 prey/day per ha | 2% | | |

TABLE 10 (Continued)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|--|---|---------------------------|-------------------------|---|-----------------------------|--|---|
| Avian guild (incl. BCCH, BOCH, RBNU, BRCR, and 20 other non-WT species) | Eastern spruce budworm | END | L, P | BCCH: 2120 prey/ha per season BOCH: 890 prey/ha per season RBNU: 1760 prey/ha per season | 84% | Crawford and Jennings 1989; Crawford et al. 1990 | Mortality estimated for entire guild. RBNU: positive functional response to increased prey density. Conclude: birds are capable of reducing growth loss in spruce-fir forests and dampening the severity of budworm infestations when habitats are suitable for supporting adequate numbers of avian predators. |
| | | TR | L, P | BRCR: 0 prey/ha per season | 22% | | |
| Avian guild (incl. BCCH, MOCH, and 24 non-WT species) | Western spruce budworm (<i>Choristoneura occidentalis</i>) | — | L, P | BCCH: 6.1 L or P/predator per hour MOCH: 6.1 L or P/predator per hour | — | Garton 1987 | Conclude: BCCH and MOCH play a role in maintaining sparse budworm densities during intervals between outbreaks. |
| Avian guild (incl. MOCH, RBNU) | Western spruce budworm | EPI | L, P | — | 66–72% | Torgerson and Campbell 1982; Takekawa and Garton 1984 | Mortality estimated for entire guild (? species). Conclude: birds contribute significantly to regulation of budworm populations. |
| Order Hymenoptera | | | | | | | |
| Avian guild (incl. BCCH, DOWO) | European pine sawfly (<i>Neodiprion sertifer</i>) | END | L | — | 95% | Coppel and Sloan 1971 | Mortality estimated for entire guild (? species). Conclude: resident birds (e.g., BCCH, DOWO) are most important in control of sawfly densities. |

TABLE 10 (Concluded)

| Predator ^a | Prey | Prey density ^b | Prey stage ^c | Predator consumption ^d | Prey mortality ^e | Source | General comments/ conclusions |
|--------------------------------------|---|---------------------------|-------------------------|--|-----------------------------|-----------------------------|---|
| Avian guild (incl. BCCH, YBSA) | Larch sawfly (<i>Pristiphora erichsonii</i>) | END | L, A | — | 5.9% L; 64.9% A | Buckner and Turnock 1965 | Mortality estimated for entire guild (? species). BCCH and YBSA: functional and numerical response to increased prey density. Conclude: birds are most likely to impact prey at low prey densities. |
| | | TR | L, A | BCCH: 1054 A/predator per season YBSA: 76 L/predator per season | 0.5% L; 5.6% A | | |

^a Predators are abbreviated according to species codes in Cannings and Harcombe (1990): BBWO = Black-backed Woodpecker; BCCH = Black-capped Chickadee; BOCH = Boreal Chickadee; BRCR = Brown Creeper; CBCH = Chestnut-backed Chickadee; COGR = Common Grackle; DOWO = Downy Woodpecker; HAWO = Hairy Woodpecker; MOBL = Mountain Bluebird; MOCH = Mountain Chickadee; PIWO = Pileated Woodpecker; PYNU = Pygmy Nuthatch; RBNU = Red-breasted Nuthatch; TTWO = Three-toed Woodpecker; VGSW = Violet Green Swallow; WHWO = White-headed Woodpecker; YBSA = Yellow-bellied Sapsucker; non-WT species = species that are not considered wildlife tree users.

^b Prey density = codes: END = endemic; EPI = epidemic; PAN = panepidemic; TR = transitional.

^c Prey stage = prey life cycle stage (A = adult; C = cocoon; E = egg; L = larvae; P = pupae).

^d Predator consumption = rate of prey consumption by the predator.

^e Prey mortality = rate of prey mortality attributed to the predator.

TABLE 11 Summary of quantitative studies of mammalian predation on forest pests

| Predator | Prey | Prey density ^a | Prey stage ^b | Predator consumption ^c | Prey mortality ^d | Source | General comments/ conclusions |
|---|------------------------|---------------------------|-------------------------|-----------------------------------|-----------------------------|-------------------------------|---|
| <u>Order Lepidoptera</u> | | | | | | | |
| Deer Mouse | Gypsy moth | EPI | P | 28 P/predator per day | — | Smith and Lautenschlager 1981 | Consumption estimate based on metabolic requirements. Possibly a weak numerical response to increased moth density. |
| Red Squirrel, Least Chipmunk | Jack pine budworm | END | L, P | — | — | Mattson et al. 1968 | Found negligible budworms in analysis of stomach contents of 10 chipmunks. Conclude: small mammals are not important budworm predators. |
| | | EPI | L, P | — | — | | |
| Red Squirrel | Eastern spruce budworm | EPI | L, P | 400–500 prey/predator per day | — | Dowden et al. 1953 | Budworms made up 51% of red squirrel diet. Conclude: red squirrels could contribute to control of budworm densities. |
| Red Squirrel | Eastern spruce budworm | — | L, P | 600–700 prey/predator per day | — | Morris 1963 | Estimate based on laboratory feeding trials; no alternate prey available. |
| Red Squirrel | Eastern spruce budworm | EPI | L, P | 0–39 prey/predator stomach | — | Jennings and Crawford 1989 | Estimate based on stomach content analyses. Consumption was lower than previously estimated potential consumption. |
| Small mammal guild (incl. Red-backed Vole) | Eastern spruce budworm | EPI | L, P | — | — | Jennings et al. 1991 | Digestive tracts of 2 Red-backed Voles examined contained no budworm larvae or pupae although other guild members did. |

TABLE 11 (Continued)

| Predator | Prey | Prey density ^a | Prey stage ^b | Predator consumption ^c | Prey mortality ^d | Source | General comments/ conclusions |
|---|--------------|---------------------------|-------------------------|-----------------------------------|-----------------------------|--------------|--|
| <u>Order Hymenoptera</u> | | | | | | | |
| Small mammal guild (incl. Deer Mouse and 2 other non-WT species) | Pine sawfly | END | C | 25 C/predator per day | 5% | Holling 1959 | Mortality estimated for entire guild (3 species). Deer Mouse: functional and numerical response to increased prey density. Conclude: small mammals can theoretically control or dampen oscillations in sawfly densities. |
| | | TR | C | 135 C/predator per day | 15% | | |
| | | EPI | C | 240 C/predator per day | 14% | | |
| Small mammal guild (incl. Red-backed Vole) | Larch sawfly | — | C | ≤600 C/predator per day | — | Buckner 1955 | Study inconclusive; the role of small mammal predation on sawflies requires further evaluation. |

^a Prey density codes: END = endemic; TR = transitional; EPI = epidemic.

^b Prey stage = prey life cycle stage; codes used: L = larvae; P = pupae; C = cocoon.

^c Predator consumption = rate of prey consumption by the predator.

^d Prey mortality = rate of prey population mortality attributed to the predator or predator guild.

4 MANAGEMENT IMPLICATIONS FOR WILDLIFE TREE USERS

Wildlife tree-dependent insectivorous birds, bats, and small mammals are of potential economic importance because of their food habits and their capacity to consume large amounts of injurious forest insects. Although these biological agents interact with a host of other factors to influence the abundance and distribution of forest pest populations, managing for healthy, sustainable populations of insectivorous predators can be cost effective (Takekawa et al. 1982; Takekawa and Garton 1984; Garton et al. 1984). The value of forest birds in the biological control of spruce budworm alone in Douglas-fir stands in Washington is estimated at \$18.15 per hectare (Garton et al. 1984). Furthermore, natural predators reduce our growing dependence on pesticides to control forest pests (DeGraaf 1977; Miller 1985; Lousier 1989).

The quantitative effect of bark-foraging and foliage-gleaning birds on forest pest populations is clearly documented and these groups should be considered a priority for management. All are primary cavity excavators except the Brown Creeper. The response of primary cavity excavators to insect outbreaks is partly limited by the availability of suitable nesting habitat (Kroll and Fleet 1979; Moeck and Safranyik 1984). To meet the nesting, roosting and feeding requirements of these species, wildlife trees of sufficient diameter, height and density and appropriate species and decay classes must be retained (Mannon et al. 1980; Raphael and White 1984; Zarnowitz and Manuwal 1985; Lundquist 1988). Although some of these factors vary according to species-specific requirements, primary cavity excavators generally prefer to nest in large-diameter snags with decayed heartwood and broken tops (Conner et al. 1976; Mannon et al. 1980; Raphael and White 1984; Neitro et al. 1985; Lundquist 1988; Harestad and Keisker 1989; Lundquist and Mariani 1991). Management guidelines for the retention of wildlife trees of sufficient size and density to support cavity-nesting bird populations are discussed in Thomas et al. (1979), Mannon et al. (1980), Raphael and White (1984), Neitro et al. (1985), Zarnowitz and Manuwal (1985), Lundquist (1988), Wildlife Tree Committee of British Columbia (1992) and Steeger et al. (1993).

In addition to snag management, silvicultural practices favouring primary cavity excavators include reducing the size of clearcuts (Kroll et al. 1980), altering the shape of clearcuts to generate long, narrow openings (Kroll et al. 1980), increasing the rotation age (Kroll et al. 1980; Raphael and White 1984; Keisker 1987) and retaining old-growth forest islands until the harvested stand regenerates (Raphael and White 1984). The spatial distribution of these islands and their proximity to other mature or old-growth stands should also be considered (Lousier 1989). Uneven-aged management or periodic thinning to create openings in the canopy for regeneration of deciduous trees is also advocated (Crawford et al. 1983; Keisker 1987).

Food supply between insect outbreaks may also limit the density of primary cavity excavators (Kroll et al. 1980; Moeck and Safranyik 1984), who forage on a variety of substrates such as standing dead or live trees, stumps, downed logs and woody debris. Foraging methods and associated foraging habitat requirements change seasonally (Jackson 1970; Conner 1979; Bull 1980; Lundquist and Manuwal 1990), and in winter, standing trees are the primary foraging substrate (Conner et al. 1975; Bull and Meslow 1977; Bull 1980). Woodpeckers prefer snags as foraging substrates (Raphael and White 1984; Lundquist and Manuwal 1990); however, they may tolerate more size and decay stage variation in feeding trees than in nesting trees (Mannon et al. 1980; Raphael and White 1984; Bull 1987; Swallow et al. 1988; Steeger et al. 1993). Brown Creepers, Red-breasted Nuthatches and Pygmy Nuthatches use live trees and snags in proportion to their respective occurrence (Raphael and White 1984; Lundquist and Manuwal 1990), while Chestnut-backed Chickadees prefer live trees over snags as foraging substrate.

Bark-foraging primary cavity excavators generally prefer large-diameter trees (i.e., > 50 cm at breast height as foraging substrate) (Mannon et al. 1980; Bull 1987; Swallow et al. 1988; Lundquist and Manuwal 1990; Mariani and Manuwal 1990; Steeger et al. 1993). A preference for tree species with deeply furrowed bark such as Douglas-fir is also shown by some species (Lundquist and

Manuwal 1990; Mariani and Manuwal 1990). Trees of large diameter with furrowed bark provide optimal temperature and moisture conditions for insect larvae and pupae to overwinter, and support a greater abundance and diversity of insects (Jackson 1979b; Bull 1987; Mariani and Manuwal 1990). They also increase the available foraging substrate without increasing a bird's area-of-search for prey (Mariani and Manuwal 1990). Therefore, by preferring deeply furrowed, large-diameter trees, birds can reduce their energetic costs of foraging (i.e., search and travel costs).

Primary cavity excavators should be provided with sufficient numbers of standing, large-diameter feeding trees, in addition to those required for nesting (Lundquist 1988; Steeger et al. 1993). This will sustain woodpecker population densities during periods of low food availability (e.g., winter, between insect outbreaks). The spatial distribution of feeding trees within a stand must also be considered. A closely clumped pattern of feeding patches may be advantageous, both to satisfy the cover requirements of foraging birds and to minimize the travel time within and between patches (Raphael and White 1984).

Other options to enhance the food supply of primary cavity excavators include maintaining standing snags or killing trees to increase populations of secondary insects (Koplin 1972), culturing and dispersing insects eaten by these species in areas susceptible to insect outbreaks (Koplin 1972), high-stumping to provide additional foraging substrate (Kroll et al. 1980, Moeck and Safranyik 1984), and treating trees with herbicide to enhance the foraging efficiency of woodpeckers (Bergvinson and Borden 1992). To ensure an adequate supply of alternative food sources (e.g., berries, nuts, seeds), limiting post-harvest site preparation and vegetation control are also suggested (Kroll et al. 1980).

Less is known about the roosting habitat requirements of cavity nesters (Backhouse and Lousier 1991). Nesting and roosting requirements may differ for individual species (Bull et al. 1992) and providing suitable nesting habitat does not necessarily ensure that roosting habitat is adequate.

By meeting the habitat requirements of primary cavity excavators, it is generally assumed that the habitat needs of other wildlife tree-dependent groups are also met (Thomas et al. 1979; Neitro et al. 1985). Providing nest boxes for insectivorous

secondary cavity-using birds is a common management technique in Europe (Thomas et al. 1975; McFarlane 1976; Otvos 1979). Increases in bird density and diversity and decreases in lepidopteran larval densities (compared to control areas) have been associated with this technique (see references in Takekawa et al. 1982). Although nest boxes should not be considered as an alternative to snag management (Mannon et al. 1980; Brawn and Balda 1983), they may be useful to enhance populations of secondary cavity users in chronic outbreak areas (Langelier and Garton 1986).

Horizontal and vertical diversity should be considered to enhance the habitat for aerial-foraging and ground-foraging secondary cavity users (Langelier and Garton 1986). Thinning of dense stands, group selection cutting or interspersing small- to medium-sized clearcuts throughout a stand will provide different degrees of canopy closure and augment the shrub understorey for these species (Garton and Langelier 1983).

Species-specific habitat requirements for bats have yet to be established in British Columbia; however, some roosting and foraging requirements are common to a number of species. Wildlife tree-dependent bats use tree hollows and cavities or cracks in and under tree bark for roosting (Fitch and Shump 1979; Kunz 1982; Barclay 1985; van Zyll de Jong 1983; Barclay et al. 1988; Nagorson and Brigham 1993). Studies in Oregon (Perkins and Cross 1988) and in coastal forests of the Pacific Northwest (Thomas 1988) indicate that bats prefer to roost in Douglas-fir/western hemlock stands that exceed 200 years of age. Preference for this age class is linked to bark crevices, which first appear at about 80 years and become apparent in trees of 150 years or older, and to snag density (Perkins and Cross 1988). Snag management for suitable species, ages, decay classes and densities of roosting trees is critical to maintain viable populations of insectivorous bats.

Bat activity patterns near roost sites led Thomas (1988) to conclude that although old-growth stands are critical for roosting, bats may be foraging in younger age classes. Edge habitat and habitat near water are considered important foraging habitat elements (Mayle 1990). To improve bat foraging habitat, travel corridors with an abundant shrub layer and sheltered areas around riparian zones should be maintained (Mayle 1990).

To ensure viable populations of small mammals

that will disperse mycorrhizal inoculum, coarse woody debris (e.g., logs, stumps, root wads, bark, piles of limbs) must be available as well as wildlife trees. These features are used for thermal protec-

tion and cover, reproduction, feeding, food storage and as runways. Through appropriate management of wildlife trees, requirements for coarse woody debris should also be satisfied (Maser et al. 1979).

5 DIRECTIONS FOR FUTURE RESEARCH

5.1 Primary Cavity Excavators

The studies reviewed here clearly document that primary cavity excavators have a significant beneficial effect on the abundance and distribution of forest pests. Therefore, management goals should promote and maintain healthy, sustainable populations of these insectivorous predators. Emphasis should be placed on research that determines:

1. the density, size, decay stage, species and associated characteristics of wildlife trees required to meet the specific nesting, foraging and roosting requirements of each primary cavity excavator; and
2. the effectiveness of different silvicultural systems and practices in meeting these habitat requirements in representative biogeoclimatic zones across the province.

The latter could be addressed through comparative or experimental studies that investigate the reproductive success and foraging energetics of woodpeckers nesting in areas with different harvesting regimes. Useful and feasible parameters to measure include fledging success, food delivery rates to nestlings and energy expenditure of breeding woodpeckers.

Primary cavity excavator habitat research has mainly focused on nesting requirements and on foraging behaviour during the breeding or post-breeding season. However, winter may represent an energetic bottleneck due to the lack of flying insects and because ground-based foraging substrate is snow-covered. The capacity of the habitat to meet each species' winter food requirements must be evaluated. Research which integrates the management of pests and predators with operational forestry is also needed. The effects of current pest management practices (fire suppression and salvage harvesting, pheromone baiting, pesticide application) on predator populations need to be

evaluated. Modified silvicultural systems which potentially enhance the efficiency of natural predators should be developed and tested in operational trials.

5.2 Secondary Cavity Users

Although secondary cavity users do consume injurious insects, their quantitative effect on forest pests in the Pacific Northwest is not well studied. Future research should investigate the degree of dietary opportunism shown by various species in response to changes in pest insect density. This type of research can be facilitated by encouraging predators (e.g., Tree Swallows, Violet-green Swallows, Western Bluebirds, Mountain Bluebirds, House Wrens) to use nest boxes and by using specialized techniques for diet determination (e.g., cameras, artificial nestlings). Through comparative studies of different pest densities or by artificially stocking pests, the effect of pest density on the diet, foraging behaviour and reproductive success of secondary cavity users can be investigated. An excellent example of this type of research initiative is Dahlsten and Copper's (1979) study of Mountain Chickadee predation on the Douglas-fir tussock moth in northeastern California.

5.3 Bats

Studies of the effect of bats on forest pest insects are lacking, presumably because of the difficulties in observing and measuring predation in nocturnal aerial insectivores. Such research should be conducted in the broader context of species-specific foraging behaviour, foraging habitat requirements and prey selection. By measuring insect density and diversity while concurrently monitoring the foraging activity and diet of bats, inferences can be made about the degree of selectivity or opportunism shown by different species. Radiotelemetry

could be used to monitor the foraging activity of larger species; smaller species could be marked with light tags and their foraging observed. Fecal analysis would provide an indication of diet composition and breadth.

Comparative studies of the foraging behaviour and prey selection of different bat species in areas of endemic versus epidemic pest densities (e.g., emergent mountain pine beetles) would establish to what extent pest species are included in the diet. Parameters that could be measured include the number of feeding passes and buzzes, time spent away from the roost, and diet composition and breadth.

5.4 Small Mammals

Few quantitative studies of small mammal predation of insects exist, presumably because of observational difficulties. An alternative approach would be to study small mammal foraging behaviour in outdoor enclosures where a natural feeding environment can be mimicked while pest densities can be readily manipulated and predation rates quantified. This would allow the effect of other habitat elements (e.g., forest cover, coarse woody debris) on foraging behaviour and diet selection to be examined concurrently.

APPENDIX 1 FOREST INSECT PESTS AND THEIR ASSOCIATED TAXONOMIC CLASSIFICATION

| Common name | Order | Family |
|-----------------------------|--------------|----------------|
| Ant | Hymenoptera | Formicidae |
| Bark beetle | Coleoptera | Scolytidae |
| Black-headed budworm | Lepidoptera | Tortricidae |
| Codling moth | Lepidoptera | Olethreutidae |
| Douglas-fir tussock moth | Lepidoptera | Liparidae |
| Eastern spruce budworm | Lepidoptera | Tortricidae |
| Engelmann spruce beetle | Coleoptera | Scolytidae |
| Engraver beetle | Coleoptera | Scolytidae |
| European pine sawfly | Hymenoptera | Tenthredinidae |
| Forest looper | Lepidoptera | Geometridae |
| Geometer moth | Lepidoptera | Geometridae |
| Gypsy moth | Lepidoptera | Liparidae |
| Hardwood borer | Coleoptera | Buprestidae |
| Ips beetle | Coleoptera | Scolytidae |
| Jack pine budworm | Lepidoptera | Tortricidae |
| Larch casebearer | Lepidoptera | Coleophoridae |
| Larch sawfly | Hymenoptera | Tenthredinidae |
| Leaf bug | Hemiptera | Miridae |
| Locust | Orthoptera | Acrididae |
| Lodgepole needle miner | Lepidoptera | Gelechiidae |
| Long-horned beetle | Coleoptera | Cerambycidae |
| Metallic wood-boring beetle | Coleoptera | Buprestidae |
| Mountain pine beetle | Coleoptera | Scolytidae |
| Needle miner | Lepidoptera | Gelechiidae |
| Oregon fir sawyer | Coleoptera | Cerambycidae |
| Pine sawfly | Hymenoptera | Tenthredinidae |
| Round-headed wood-borer | Coleoptera | Cerambycidae |
| Sawfly | Hymenoptera | Tenthredinidae |
| Southern pine beetle | Coleoptera | Scolytidae |
| Spruce aphid | Homoptera | Aphididae |
| Spruce beetle | Coleoptera | Scolytidae |
| Spruce budworm | Lepidoptera | Tortricidae |
| Tent caterpillar | Lepidoptera | Lasiocampidae |
| Tortricid moth | Lepidoptera | Tortricidae |
| Weevil | Coleoptera | Curculionidae |
| Western pine beetle | Coleoptera | Scolytidae |
| Western spruce budworm | Lepidoptera | Tortricidae |

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