

The ecological role of tree-dwelling mammals in western coniferous forests

Three groups of mammals that occur in coniferous forests of western North America are closely associated with large healthy, decaying, or dead trees: bats, arboreal rodents, and forest carnivores. Detailed descriptions of the ecological relations of these species are presented elsewhere in this book (Buskirk and Zielinski 2003, Hayes 2003, Smith et al. 2003). Although many other kinds of mammals use large vertical forest structures to some degree, these are the species groups that depend on them to meet their life history requirements. Consequently, these are also the mammals that are most likely to suffer population declines in forests where these structures are reduced in abundance. The need to provide for large snags and decadent trees in managed forests to maintain populations of cavity-using birds and mammals has received much attention in the literature (e.g., Balda 1975, Thomas 1979, Hoover and Wills 1984, Brown 1985). However, the perceived consequences of providing inadequate numbers and sizes of these structures in managed forests have generally been limited to the decline or loss of the wildlife species that depend on them. The broader ecological consequences that could also result from the loss or decline of tree-dwelling birds and mammals have received relatively little attention (but see Machmer and Steeger 1995, Aubry and Raley 2002).

Managing forests primarily for timber production often involves not only the removal of a substantial proportion of large, healthy trees from each harvest unit, but also the elimination of large dead or decadent trees. Retaining tall, large-diameter snags or decaying live trees during timber

harvest operations involves substantial safety risks (Styskel 1983, Hope and McComb 1994) that often result in the removal of these structures, even when options are available for retaining them in leave patches (Aubry and Raley 2002). Consequently, although forest-management plans may involve green-tree retention harvests and prescriptions for preserving key dead and decadent structures in harvest units, the latter goals may be very difficult to attain. Thus, mammals that are closely associated with large, vertical forest structures may suffer population declines or extirpation in intensively managed forest landscapes.

The recent emergence of ecosystem management as a guiding principle for conservation (e.g., Boyce and Haney 1997) has led some ecologists and resource managers to move away from focusing only on the management of habitat to maintain populations of key wildlife species. Increasingly, wildlife managers are being encouraged to go beyond this narrow focus and consider how ecosystems could be managed to provide for ecological integrity, not simply to provide habitat for one or several sensitive wildlife species (Marcot 1996, Marcot et al. 1998, Marcot and Aubry 2003). For example, a recently published synthesis of wildlife biology, ecology, and resource management in the Pacific Northwest (Johnson and O'Neil 2001) was much more than an update of previous summaries of wildlife-habitat relationships (Thomas 1979, Brown 1985); it also included explicit consideration of the ecological roles that wildlife species may play in the ecosystems they occupy, i.e., their "key ecological functions". However, the matrices of key ecological functions included in this synthesis (O'Neil et al. 2001) were based partly on professional judgments and expert opinion (Marcot and Vander Hayden 2001), and represent only a categorical summarization of known and hypothesized ecological roles that vertebrate and invertebrate organisms may play in northwestern ecosystems. No comprehensive assessment of the contributions that tree-dwelling mammals may make to the composition, structure, and function of western coniferous forest ecosystems has been conducted.

The purpose of this chapter is to present what we believe are the most important ecological roles that each group of tree-dwelling mammals may play in western forests, and review available literature that provides empirical support for each hypothesized role. We consider 14 species of bats, 11 species of arboreal rodents, and six species of carnivores to be associated with large healthy, decaying, or dead trees in coniferous forests of western North America (Table 12.1). The chapter is divided into four major sections: in the first three sections, we discuss the primary ecological

Table 12.1. Mammals associated with large trees in coniferous forests of western North America

Bats	Arboreal rodents	Forest carnivores
Silver-haired bat (<i>Lasionycteris noctivagans</i>)	Northern flying squirrel (<i>Glaucomys sabrinus</i>)	Black bear (<i>Ursus americanus</i>)
Hoary bat (<i>Lasiurus cinereus</i>)	Douglas squirrel (<i>Tamiasciurus douglasii</i>)	Raccoon (<i>Procyon lotor</i>)
Western red bat (<i>L. borealis</i>) ^a	Red squirrel (<i>T. hudsonicus</i>)	Ringtail (<i>Bassariscus astutus</i>)
Big brown bat (<i>Eptesicus fuscus</i>)	Western gray squirrel (<i>Sciurus griseus</i>)	Fisher (<i>Martes pennanti</i>)
Pallid bat (<i>Anrozous pallidus</i>)	Arizona gray squirrel (<i>S. arizonensis</i>) ^a	American marten (<i>M. americana</i>)
Townsend's big-eared bat (<i>Corynorhinus townsendii</i>) ^b	Abert's squirrel (<i>S. aberti</i>) ^a	Western spotted skunk (<i>Spilogale gracilis</i>)
Long-eared myotis (<i>Myotis evotis</i>)	Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	
Keen's myotis (<i>M. keenii</i>)	Bushy-tailed woodrat (<i>N. cinerea</i>)	
Northern long-eared myotis (<i>M. septentrionalis</i>)	Red tree vole (<i>Arborimus longicaudus</i>)	
Long-legged myotis (<i>M. volans</i>)	Sonoma tree vole (<i>A. pomoi</i>) ^a	
California myotis (<i>M. californicus</i>)	Porcupine (<i>Erethizon dorsatum</i>)	
Little brown myotis (<i>M. lucifugus</i>)		
Fringed myotis (<i>M. thysanodes</i>)		
Yuma myotis (<i>M. yumanensis</i>)		

^a Species does not occur in Washington and Oregon.

^b Townsend's big-eared bats are listed as associated with large trees in this chapter based on their apparent use of hollow redwoods (Gellman and Zielinski 1996).

roles that each species group may play in western coniferous forests; and in the last, we focus on the subset of tree-dwelling mammals that occur in coniferous forests of Washington and Oregon, and use the key ecological functions provided by O'Neil et al. (2001) to present an example of how information on the ecological contributions of individual species could be used by managers to compare the effects of alternative forest-management strategies on ecosystem function.

Bats

Bats comprise a substantial amount of the mammalian species richness in most western coniferous forests. Although quantitative estimates of their population densities in western forests are not available (see Hayes 2003), bats appear to be locally abundant in many areas. As a consequence of their abundance and specialized ecological niches, it is likely that bats play significant ecological roles in western coniferous forests (Marcot 1996). Despite substantial recent advances in our understanding of the habitat ecology of bats (see Hayes 2003), relatively little work has been conducted that directly examines the functional roles played by bats in forests. Consequently, the magnitude of their contributions to the functioning of western coniferous forest ecosystems remains speculative. We consider three potential ecological roles of bats in western coniferous forests: as predators of insects, as prey of other vertebrates, and as agents of nutrient transport.

Bats as predators of insects

Probably the most significant functional role played by bats in western coniferous forests is as predators of insects. Bats are often purported to play an important role in controlling insect populations (especially in agricultural systems; e.g., Whitaker 1993, 1995, Long 1996, Long et al. 1998). Although it is likely that bats significantly impact insect populations, this conclusion is based largely on expert opinion and logical argument, not scientific research. We are not aware of any studies that have directly examined the influence of bat predation on abundance, population dynamics, or demographics of insects. Assertions that bats play an important ecological role in predation of insects in western coniferous forests are based primarily on information about the types and amounts of prey consumed by bats. All of the bats associated with western coniferous forests (see Hayes 2003) are insectivorous (Black 1974, Whitaker et al. 1977, 1981*a,b*, Barclay 1985, Rolseth et al. 1994, Wilson and Ruff 1999). Most are aerial insectivores that feed on nocturnal flying insects, although

some species also regularly glean insects and other invertebrates from the ground or vegetation.

Obtaining accurate estimates of the amounts of prey consumed by bats is challenging. Amounts and types of prey consumed vary with prey availability (Brigham and Saunders 1990, Hickey and Fenton 1996), time of night (Whitaker et al. 1996, Best et al. 1997), and with the species (Black 1974, Whitaker et al. 1977, 1981*a,b*), sex, reproductive status (Kunz 1974, Kurta et al. 1989, 1990, Kunz et al. 1995, McLean and Speakman 1999), and age (Kunz 1974, Rolseth et al. 1994, Hamilton and Barclay 1998) of bats. A variety of approaches have been used to estimate the amount of prey consumed, including direct observation (e.g., Hickey and Fenton 1990, 1996), comparison of pre- and post-flight body mass (e.g., Kunz 1974, Anthony and Kunz 1977, Kunz et al. 1995), use of doubly labeled water (e.g., Kurta et al. 1989, 1990), and fecal sample analysis (e.g., Whitaker and Clem 1992, Whitaker 1995). However, each of these approaches has inherent limitations and assumptions that affect estimates. For example, Barclay et al. (1991) hypothesized that overestimation of digestive efficiency in some studies has resulted in substantial underestimation of the biomass of prey consumed by bats.

Early estimates of foraging intensity by bats were based on the mass of stomach contents in bats shot while foraging, body mass of insects that were considered to be primary prey species, and observations and assumptions about the foraging behavior of bats. These studies estimated the number of insects consumed to be as high as 100 to 500 insects per hour (or 1.6–8.3 insects/minute; Gould 1955, 1959). This rate is comparable to feeding rates estimated by others (1.5–9.5 insects/minute, Griffin et al. 1960; 7 insects/minute, Anthony and Kunz 1977). Because the rate of insect consumption varies both temporally and with the type of prey, however, extrapolating these figures to nightly consumption rates should be done with caution. Estimates of total biomass consumed per night is probably a more reliable approach to estimating total consumption (Table 12.2). The cumulative consumption of insects by bats is impressive. Based on fecal sample analyses, Whitaker and Clem (1992) estimated that a colony of 300 evening bats (*Nycticeius humeralis*) in Indiana would consume 6.3 million insects per year. Whitaker (1995) estimated that a colony of 150 big brown bats in the same region would consume roughly 1.3 million insects per year.

To our knowledge, estimates of the amount of insects consumed have not been made for bats in western coniferous forests, but the number of insects consumed is undoubtedly huge. Bats are the primary predators

Table 12.2. *Estimated nightly consumption of prey by bats*

Species	Prey consumed per night		Method of analysis	Reference
	Biomass (g)	% of body mass consumed		
Hoary bat	17.13	57	Direct observation	Hickey and Fenton (1996)
Western red bat	6.3	42	Direct observation	Hickey and Fenton (1990)
Big brown bat	17.2	99	Doubly labeled water	Kurta et al. (1990)
Little brown myotis	5.5–6.7	61–85	Doubly labeled water	Kurta et al. (1989)
Little brown myotis	2.5–3.7	31–49	Pre-post flight body mass comparison	Anthony and Kunz (1977)
Cave myotis ^{a,b}	2.0–3.4	17–30	Pre-post flight body mass comparison	Kunz (1974)
Mexican free-tailed bat ^c	4.7–8.6	39–73	Pre-post flight body mass comparison	Kunz et al. (1995)

^a *Myotis velifer*.

^b Estimated maximum daily consumption for males and females combined.

^c *Tadarida brasiliensis*.

of many species of nocturnal, flying insects, and some of the insects fed upon by bats play important ecological roles in western coniferous forests. Some, such as the western spruce budworm (*Choristoneura occidentalis*) and the Douglas-fir tussock moth (*Orygia pseudotsugata*), are considered to be forest pests, and can significantly impact wood fiber production. Although there are no estimates of the impacts of bats on these species, bats may play an important role in forest health by minimizing the impacts or outbreaks of forest pests.

Bats as prey of other vertebrates

Bats are preyed upon by a number of vertebrate predators throughout the world (Gillette and Kimbrough 1970, Speakman 1991b, Fenton 1995). Despite the importance of predation on bats in some settings, many of the anecdotal observations of predation on bats by fish, amphibians, birds, and mammals (e.g., Stager 1942, Davis 1951, Kinsey 1961, Martin 1961, Wilks and Laughlin 1961, Elwell 1962, Wiseman 1963, Barr and Norton 1965, Cleeves 1969, Lee 1969, Mumford 1969, Thomas 1974, Kirkpatrick 1982, Wroe and Wroe 1982, Yager and Williams 1988) have been published because of their uniqueness or rarity, and these observations often

represent sightings of unusual opportunistic foraging events or specialized foraging strategies developed by individual predators.

Although predation on bats sometimes occurs when bats are foraging or commuting, much of this predation occurs when bats are roosting or emerging from roosts. Large concentrations of bats at roost sites (Kunz 1982), coupled with relatively predictable patterns of emergence from roosts (Erkert 1982), provide significant opportunities for predators to prey on bats in some areas (Fenton et al. 1994). In western coniferous forests, bats typically do not congregate in very large colonies and generally exhibit low fidelity to day roosts (see Hayes 2003), reducing the potential functional significance of bats as prey. Low fidelity to roost sites may be a strategy to minimize risk of predation (Lewis 1995). Furthermore, bats may select times (Jones and Rydell 1994, Kunz and Anthony 1996, Rydell et al. 1996, Duvergé et al. 2000) and patterns (Swift 1980, Brigham and Fenton 1986; but see Speakman et al. 1992, Kalcounis and Brigham 1994) of emergence from roosts to minimize predation. Indeed, nocturnality in bats may have evolved to minimize the risk of predation (Speakman 1991a, 1995).

Regular predation on bats in temperate forests appears to be uncommon and generally restricted to a relatively small group of predators. Although diurnal raptors feed on bats during twilight hours in some parts of the world (e.g., Fenton et al. 1994), nocturnal predation by owls is the most significant predation pressure on bats in temperate regions (Speakman 1991b). Bats generally comprise a relatively small proportion of the diet of most predators. Speakman (1991b) estimated that bats represented only 0.003% of the diet of small falcons and hawks and 0.036% of the diet of owls in Great Britain. However, bats can comprise a substantial amount of the prey taken by predators that have learned to specialize on bats. For example, although bats comprise less than 1% of the diet of spotted owls (*Strix occidentalis*) in most areas (Forsman et al. 1984, Smith et al. 1999), they represented 12% of prey taken in southern Arizona (Duncan and Sidner 1990). Overall, it appears that bats probably do not play a major ecological role as prey over large geographic areas in western coniferous forests. However, there has been very little work investigating interactions between bats and predators in this region.

Bats as agents of nutrient transport

Bats may play an important ecological role in western coniferous forests by transporting nutrients, especially from riparian areas to upland areas

(Cross 1988). To our knowledge, no empirical study has estimated the amount of nutrient transfer by bats. Given the relative mobility of bats and the fact that bats often use different habitats for roosting and foraging (see Hayes 2003), it is reasonable to hypothesize that bats may play a significant role in nutrient transfer within ecosystems. Nutrient transfer has been shown to be facilitated by other species of mammals, and this can influence nutrition and nutrient content of plants (e.g., Ben-David et al. 1998). However, we suspect that the importance of nutrient transfer by bats in overall ecosystem function is probably relatively low, but may influence microsite conditions. We hypothesize that the ecological function of nutrient transfer is probably concentrated in relatively small areas, such as the area in, under, or immediately surrounding roosts.

Arboreal rodents

Rodents are an extremely diverse order of mammals that occupy a variety of ecological niches and comprise a substantial amount of the biomass and diversity in western coniferous forests. Some species exploit the forest floor for nesting and foraging, while others spend much of their time in trees; the latter group are often referred to as “arboreal” rodents (Table 12.1, see Smith et al. 2003). The red and Sonoma tree voles are considered to be the most arboreal mammals in western North America (Carey 1991). Both species are closely associated with large trees and conduct almost all of their activities high in the canopy of Douglas-fir (*Pseudotsuga menziesii*) forests (Maser et al. 1981, Gillesberg and Carey 1991, Meiselman and Doyle 1996). Red tree voles are most abundant in late-successional forests (Corn and Bury 1986, Gillesberg and Carey 1991, Meiselman and Doyle 1996) where large tree canopies interweave. At the low end of the scale of arboreal activity is the bushy-tailed woodrat, which uses cavities in standing and fallen trees. It builds nests of sticks and woody debris on branches of trees, in tree hollows, and on the ground in low-elevation transitional and mixed-conifer forests (Carey 1991). Here, we consider four potential ecological roles of arboreal rodents in western coniferous forests: as prey of other vertebrates, as disseminators of fungal spores and mistletoe seeds, as predators and disseminators of conifer seeds, and as modifiers of forest composition and structure.

Arboreal rodents as prey of other vertebrates

Arboreal rodents are preyed upon by a wide array of vertebrate predators throughout the West. Some avian predators, including the federally

listed northern spotted owl (*S. o. caurina*), consume relatively large and energetically profitable prey such as woodrats, northern flying squirrels, and red tree voles (Forsman et al. 1984, Smith et al. 1999). Northern flying squirrels comprised from 25.1% to 57.5% of the biomass consumed by spotted owls in Douglas-fir and western hemlock (*Tsuga heterophylla*) forests in western Oregon, whereas in the dry mixed-conifer and mixed-evergreen forests in the Klamath Mountains of southern Oregon, dusky-footed woodrats represented up to 69.9% of the biomass in spotted owl diets (Forsman et al. 1984). The abundance of these arboreal prey species can influence the reproductive success and densities of predators. Regional differences in densities of the northern spotted owl have been attributed to regional differences in the abundance of northern flying squirrels and dusky-footed and bushy-tailed woodrats (Carey et al. 1992). There is also a significant relationship between reproductive status and the percent biomass of woodrats in California spotted owl (*S. o. occidentalis*) diets from the San Bernardino Mountains of southern California; successful nesters consumed a greater percent biomass of woodrats than non-nesters (Smith et al. 1999).

Both species of tree voles are locally important prey for the northern spotted owl. The percent occurrence of red tree voles in regurgitated owl pellets varied in different portions of the owl's range, from a low of 3.7% of items in the northern Oregon Cascades to a high of 49.1% in the Douglas-fir/coast redwood (*Sequoia sempervirens*) zone along the southern Oregon Coast (Forsman et al. 1984). Averaging across seven study areas, the red tree vole represented 15.1% of all prey items taken by spotted owl pairs. Due to their small size relative to other arboreal rodents, however, it only provided 2% to 19% of total biomass in the owl's diet (Forsman et al. 1984). Although the northern spotted owl is probably the primary predator of red tree voles, the long-eared owl (*Asio otus*; Reynolds 1970), saw-whet owl (*Aegolius acadicus*; Forsman and Maser 1970), raccoon, marten, fisher, various corvids (Maser et al. 1981), and ringtail (Alexander et al. 1994) also prey upon them. The Steller's jay (*Cyanocitta stelleri*) is a common predator that will systematically destroy nests in search of young voles (Howell 1926).

Diurnal squirrels can be important in the diet of predators, especially during winter. The most frequently occurring item in the winter diet of marten in northwestern Montana (Marshall 1946) and north-central Washington (Newby 1951) was the red and Douglas squirrel, respectively. In lodgepole pine (*Pinus contorta*) forests of Wyoming, northern goshawk (*Accipiter gentilis*) diets may contain up to 50% red squirrels (Squires 2000).

Goshawks may also have a stabilizing influence on Abert's squirrel populations in the southwest (Reynolds 1963, Boal and Mannan 1994). Other occasional predators of diurnal tree squirrels in western coniferous forests include the red-tailed hawk (*Buteo jamaicensis*; Luttich et al. 1970), bald eagle (*Haliaeetus leucocephalus*), and lynx (*Lynx canadensis*; Aubry et al. 2000).

Arboreal rodents as disseminators of ectomycorrhizal fungi and dwarf mistletoe

Ectomycorrhizal fungi form symbiotic relationships with the root systems of conifer trees, shrubs, and other vegetation. The tree provides carbon from photosynthesis to the fungi, and the ectomycorrhizal fungi absorb minerals and nutrients from the soil and transfer them to tree roots (Smith and Read 1997). This process helps conifer trees and other woody plants uptake water and nutrients from the soil, and facilitates the transport of carbohydrates from plants into the mycorrhizosphere. Sporocarps of these hypogeous fungi (truffles) are an important food resource for many forest mammals worldwide (Whitaker 1962, Fogel and Trappe 1978, Maser et al. 1978, Viro and Sulkava 1985, Carey et al. 1992, Carey 1995, see Luoma et al. 2003). Most sporocarps consumed by arboreal rodents in western conifer forests are from ectomycorrhizal fungi that form a symbiotic association with feeder roots of trees in the Pinaceae, Fagaceae, Betulaceae, Myrtaceae, and Salicaceae (Molina et al. 1992, North et al. 1997, see Luoma et al. 2003).

Mammals are attracted to hypogeous fungi by aromatic compounds produced by the maturing sporocarps (Fogel and Trappe 1978). Animals unearth the truffles and consume all or part of the sporocarps including the spores (Trappe and Maser 1976, Fogel and Trappe 1978). Fungal spores pass through the digestive tract unharmed and are deposited in feces in the forest soil at new locations (Trappe and Maser 1976). Although the nitrogen concentration of sporocarps is high, much of this nitrogen is in non-protein forms or is associated with cell walls, suggesting that fungal sporocarps may be low in nutritional value or protected from mammalian digestive enzymes (Claridge et al. 1999). The nutritional value of fungi to tree-dwelling mammals is largely unstudied; however, Cork and Kenagy (1989) found that one species of truffle (*Elaphomyces granulatus*) provided few nutritional benefits to the Cascade golden-mantled ground squirrel (*Spermophilus saturatus*) due to low digestibility of the sporocarps. Although they are apparently low in nutritional benefits, truffles may

be consumed simply because they are seasonally abundant and highly detectable due to the strong odor they develop when mature. Sporocarps may also be an important source of water in some regions or during certain seasonal periods because of their high moisture content (Fogel and Trappe 1978).

In western coniferous forests, many species of arboreal rodents, especially the northern flying squirrel and Douglas squirrel, contribute to forest ecosystem processes by consuming fungi and dispersing fungal spores (Maser and Maser 1988). Diets of the northern flying squirrel in the Pacific Northwest include primarily fungi and lichens (Maser et al. 1986, McIntire and Carey 1989). Northern flying squirrels consumed 12 taxa of fungi during a single season (McIntire and Carey 1989) and up to 20 taxa annually, including Basidiomycetes, Ascomycetes, and Zygomycetes (Maser et al. 1986). Both squirrel species were found to be more abundant in old forests than in managed forests (Volz 1986, Carey et al. 1992, Witt 1992, Zabel and Waters 1997) where fungal abundance and diversity were higher. Douglas and red squirrels are adept at detecting hypogeous fungi, and Douglas squirrels are reported to eat a wider array of fungi (89 species) than any other mycophagist (Fogel and Trappe 1978).

Dissemination of the spores of hypogeous fungi can only occur through the foraging activities of animals. Thus, despite the conclusion that truffles are only of moderate nutritional value for most small mammals (Claridge et al. 1999), arboreal rodents appear to be important dispersal agents for these fungi. By doing so, arboreal rodents enhance their own food supply and disseminate the ectomycorrhizal fungi that are important for the growth and survival of conifers in western forests.

Arboreal rodents may also aid in the dispersal of other plant propagules. For example, arboreal rodents have been suggested as potential long-distance dispersal agents for dwarf mistletoe (*Arceuthobium* spp.) seeds (Hawksworth et al. 1987, Hawksworth and Wiens 1996). Parasitism of conifer trees by dwarf mistletoes can have a dramatic effect on the structure and function of both individual trees and forest stands, and sets in motion a complex web of interactions with disease organisms, decay fungi, arthropods, birds, and mammals (Hawksworth and Wiens 1996, Mathiasen 1996). Arboreal rodents often use witches' brooms caused by dwarf mistletoes for nests, rest sites, and cover (Lemons 1978, Smith 1982, Tinnin et al. 1982). Dwarf mistletoes disperse seeds by an explosive mechanism that forcibly expels a single, sticky seed from the fruit as far as 16 m away (Hawksworth and Wiens 1996). Although many species of

birds and mammals feed on dwarf mistletoes, seeds lose their viability after being ingested (Hudler et al. 1979). Thus, dispersal of dwarf mistletoes by animals, and long-distance dispersal in general, is believed to occur only via external transport by birds and mammals (Hudler et al. 1979, Hawksworth et al. 1987). Few studies have been conducted to assess the ecological importance of mammals as dispersal agents of dwarf mistletoes, but seeds have been found on the fur of the least chipmunk (*Tamias minimus*), golden-mantled ground squirrel (*Spermophilus lateralis*), red squirrel, northern flying squirrel, and marten (Ostry et al. 1983, Hawksworth et al. 1987). In British Columbia, Canada, one in 15 red squirrels examined had dwarf mistletoe seeds in its fur (Hawksworth et al. 1987), suggesting that dispersal of mistletoe seeds by arboreal rodents may occur relatively frequently.

Arboreal rodents as predators and disseminators of conifer seeds

Douglas and red squirrels feed primarily on conifer seeds and are behaviorally and anatomically adapted to exploit them (Smith 1970, 1981). Their food habits are generally similar except that red squirrels are adapted to feed on serotinous cones that remain closed on the tree, whereas Douglas squirrels are not (Smith 1970). Douglas and red squirrels are so dependent on conifer seeds for survival that their population densities fluctuate with conifer cone crops (Smith 1970). These squirrels do not hibernate and rely on cones stored in large caches to survive the harsh winter conditions that occur in many coniferous forest habitats (Lindsay 1986). The caching behavior of Douglas and red squirrels can have a significant effect on the amount and distribution of conifer seeds available for germination. Red squirrels may collect and cache enough cones to support themselves through one or more years of poor cone crops. Red squirrel caches in Alaska contained up to 8500 cones (Smith 1968), caches in the Rocky Mountains were 30–45 cm deep (Finley 1969), and caches may contain up to 24 bushels of cones in the southwest (Patton and Vahle 1986). These large caches are not covered, and seeds may remain viable for many years (Shaw 1936). Douglas squirrels generally use smaller cone caches, that may include as few as 30 cones (Carey 1991). In California, Douglas squirrels cache only enough cones to last through the winter and early spring (Koford 1982). These cone caches or “middens” function to concentrate nutrients, and probably provide food for a wide variety of

organisms. Middens are also reported to be particularly important ecological features for the American marten because they facilitate access to the subnivean layer, provide resting sites that may be energetically important in winter, and serve as natal denning sites (Buskirk and Ruggiero 1994). In lodgepole pine/spruce-fir forests of southern Wyoming, red squirrel middens were used by martens for natal den sites more than any other structure (Ruggiero et al. 1998).

Cone caching by Douglas and red squirrels can seriously interfere with natural re-seeding in some areas because the entire cone crop may be collected in poor cone years (Finley 1969). In ponderosa pine (*Pinus ponderosa*) and lodgepole pine forests, red squirrels may harvest up to 67% of mature ponderosa pine cones and remove an additional 14% before they are ripe (Schmidt and Shearer 1971). In ponderosa pine forests of the Southwest, Abert's squirrel populations fluctuated in response to cycles of ponderosa pine cone production (Farentinos 1972). In addition to seeds from mature ovulate cones, Abert's squirrels also consumed significant numbers of terminal buds and fed heavily on the inner bark of pine shoots (Keith 1965). Abert's squirrels can substantially reduce cone production of ponderosa pine trees through intensive foraging on the inner bark of excised pine shoots that contain immature ovulate cones (Allred et al. 1994). The effects of this feeding behavior may reduce the potential cone crops of these forest stands by up to 20%. By shifting their foraging from the inner bark to the seeds of mature cones, Abert's squirrels effectively reduced the total cone crop by 55% (Allred et al. 1994).

Overall, cone production differs among stands, years, seasons, tree species, and individual trees (Eis et al. 1965, Fowells 1965, Smith and Balda 1979). A tree's ability to produce cones increases with age; trees in late-successional stands may produce up to 14 times more seed than trees in young stands (Buchanan et al. 1990, Carey 1991). Large fluctuations in seed production and the synchrony of cone production among western conifers resulted in parallel fluctuations in Douglas squirrel populations (Smith 1970, Buchanan et al. 1990). Years of cone failures between years of heavy seed production led to dramatic fluctuations in populations of all seed predators and allowed a large percentage of the seeds in productive years to go uneaten and be available for germination (Smith and Balda 1979). Cone caching provides a mechanism for seed transport within a stand of trees and may provide for the storage of viable seeds over several years. Thus, available evidence indicates that tree squirrels are

likely to be important vectors for the dispersal of conifer seeds in western forests.

Arboreal rodents as modifiers of forest composition and structure

Numerous studies have been conducted on damage to commercial timber plantations from rodents foraging on conifer seeds and cambium, with variable conclusions depending on the region and forest crop. Although these problems often result in efforts to control animal damage, the same behaviors that cause economic losses to commercial forests have potential functional roles in the ecosystem. Red squirrels consume the vascular tissue of young lodgepole pine by peeling bark from branches and the main trunk from May to early July (Sullivan and Sullivan 1982, Kenward 1983, Sullivan and Vyse 1987) when other natural foods are unavailable. The winter diet of porcupines consists almost exclusively of cambium and phloem of saplings and small conifer trees (Sullivan et al. 1986). Foraging activities by arboreal rodents may also provide food for other species, especially during winter; foliage dropped by porcupines when snow covered the ground in Maine was eaten by both deer and rabbits (Curtis and Kozicky 1944).

Arboreal rodents may have their most significant influence on stand structure and dynamics during the sapling and pole stages of forest development (Van Deusen and Meyers 1962), because animal damage is more likely to cause tree mortality or change the growth form of individual trees in young stands. Feeding damage by arboreal rodents is usually greatest in stands with an average tree diameter less than 6.0 cm (Sullivan and Sullivan 1982). Feeding damage to sapwood and cambium can reduce the growth and vigor of a tree, increase its susceptibility to fungal attack, and eventually kill it (Sullivan and Vyse 1987). Girdling of saplings and small trees may cause significant tree mortality in plantations and naturally decrease tree stocking rates. In situations where trees are sparse and insular in distribution, porcupines may be capable of causing local extirpations of some conifer species (Gill and Cordes 1972).

The effects of foraging by arboreal rodents on the growth form of individual trees can be significant. Stripping bark from the leader causes mortality at the tops of small trees in Douglas-fir plantations. This leader mortality can result in tree death, but may have a greater ecological impact by creating defects in living trees. Re-sprouting at the top of a small conifer often results in multiple leaders that reduce the value of crop trees in

commercial forests. However, platforms created by multiple tops provide nest sites for many arboreal rodents and passerine birds; red tree voles, flying squirrels, and Douglas squirrels all build stick nests in the protected forked tops of previously damaged trees (Maser 1966, Maser et al. 1981). The increased availability of nest sites for arboreal rodents may significantly increase the diversity and abundance of beneficial ectomycorrhizal fungi in these stands. Thus, damage by arboreal rodents to young conifer stands, while economically detrimental, may introduce canopy structural diversity that sustains species richness.

Forest carnivores

Carnivores may influence the ecosystems they occupy by affecting the behavior and demography of prey and competitors, facilitating the dispersal of seeds, completing or interrupting the life cycles of pathogens and parasites, and cycling nutrients by scavenging carrion (Buskirk 1999). In addition, forest carnivores transport nutrients and contaminants within ecosystems, concentrate them at den and rest sites, and probably aid in the long-distance dispersal of dwarf mistletoes and hypogeous fungi. However, the functional significance of carnivores in ecosystems has received relatively little attention from researchers, and remains largely conjectural (Estes 1996). To our knowledge, no study of tree-dwelling carnivores in western coniferous forests has directly evaluated the effects of their activities on ecosystem function. Consequently, empirical information on the ecological significance of carnivores in forested habitats is sparse and speculative in nature. Here, we consider three potential ecological roles of tree-dwelling carnivores in western coniferous forests: as predators and competitors, as long-distance disseminators of propagules, and as hosts for parasites.

Forest carnivores as predators and competitors

Food webs are key features of all ecosystems, and predator–prey interactions are the fundamental linkages among species in each food web (Estes 1996). Some mammalian carnivores exert such a strong influence on the structure of prey communities that they function as keystone predators; such a role has been described for the sea otter (*Enhydra lutris*; Estes and Palmisano 1974), coyote (*Canis latrans*; Henke and Bryant 1999), and wolf (*C. lupus*; McLaren and Peterson 1994). Although keystone roles for tree-dwelling forest carnivores have not been proposed, this may simply reflect

a lack of research designed to elucidate the functional significance of these predators in the ecosystem.

There is little evidence, however, that tree-dwelling mammalian carnivores exert a strong influence on their prey populations. Although inferring the ecological effects of predation from food habits data is problematic, all species considered here (Table 12.1) consume a broad array of animal and plant foods and appear to be largely opportunistic in their choice of prey (see Buskirk and Zielinski 2003). Thus, the effects of predation by forest carnivores on the population dynamics or community structure of prey are probably minimal. However, there is evidence that predation by fishers on porcupines may have substantial ecological effects in forests where these species co-exist. Long-term data on the densities of fisher and porcupine populations in Michigan during the 1970's provided strong evidence that predation by fishers reduced porcupine populations to lower and more stable levels than occurred in the absence of fishers (Powell and Brander 1977, Earle 1978). Anecdotal observations on the effects of fisher predation on porcupine populations have also been reported from Wisconsin, New York, and Maine (Powell 1993).

Reports of heavy damage by porcupines to tree plantations in the Pacific Northwest was attributed to a dramatic increase in porcupine numbers resulting from the overtrapping of fisher populations (Stone 1952). One of the objectives of fisher re-introductions that occurred in Oregon (Kebbe 1961, Aubry et al. 1996), Idaho (Williams 1962), and Montana (Weckworth and Wright 1968) was to reduce damage to forest plantations by controlling porcupine populations. It has even been proposed that, during re-establishment of fishers in areas where porcupines have become unnaturally dense and where they have not been subjected to fisher predation for several decades, fishers may be capable of exterminating porcupines (Powell and Brander 1977). Porcupines can injure or kill large proportions of young conifer stands (Dodge and Borrecco 1992). Wounds resulting from porcupine feeding may expose trees to fungal infection (Sullivan et al. 1986, Eglitis and Hennon 1997), including the heart-rot decay fungi that are essential for creating hollows in trees and for softening heartwood to facilitate cavity excavation by woodpeckers (Conner et al. 1976, Bull et al. 1997). Consequently, porcupines may influence the availability of structures that are used by a wide array of secondary cavity-using birds and mammals. Sublethal porcupine injury may also affect tree vigor and growth and increase susceptibility to attack by insects (Sullivan et al. 1986). Thus, in some situations,

predation by fishers could be a mediating factor on the effects of porcupine foraging on the structure and composition of coniferous forest ecosystems.

Competitive interactions among tree-dwelling forest carnivores do not appear to have an important influence on their populations, even between the congeneric and ecologically similar marten and fisher. However, competition with fishers may have contributed to the decline of the Humboldt marten (*Martes a. humboldtensis*) in coastal areas of northern California (Krohn et al. 1997). Fishers are known to kill martens (de Vos 1952, Raine 1981), and it has been suggested that at very high fisher densities, interference competition may prevent martens from maintaining viable populations (Krohn et al. 1995). In the western mountains of North America, martens generally occur at higher elevations and in areas with deeper snowpacks than fishers (Powell and Zielinski 1994, Krohn et al. 1997). Martens have an energetic advantage over fishers when moving through soft, deep snow and are more efficient predators of winter-active small mammals in the subnivean layer (Leonard 1980, Raine 1983). Although their diets overlap extensively (Martin 1994), the smaller size of martens enables them to better exploit both subnivean and arboreal microhabitats and to be more efficient predators of microtine rodents and other small prey. In contrast, fishers are capable of killing porcupines and are better adapted to prey on snowshoe hares (*Lepus americanus*) and other medium-sized prey (Raine 1983). Thus, it appears that marten and fisher populations co-exist at the regional scale by partitioning available habitat according to snow conditions, and co-exist occasionally at the local scale by partitioning food resources.

Forest carnivores as long-distance disseminators of propagules

Forest carnivores are omnivorous, highly mobile, and generally occupy large home ranges that encompass a variety of habitat conditions. All six species of tree-dwelling forest carnivores considered here feed extensively on both animal and plant foods, especially fruits. During summer and fall, the diet of black bears is dominated by fruits and mast crops (Pelton 1982). Except during the spring, when animal matter predominates in the diet, raccoons feed more often on fruits and seeds than on other food items (Kaufmann 1982). Ringtails are less herbivorous than raccoons, but fruits are also common in ringtail diets (Toweill and Teer 1977, Alexander et al. 1994), and are important constituents of late-summer and fall diets

for both the marten (Buskirk and Ruggiero 1994) and fisher (Powell and Zielinski 1994).

Several authors have summarized the prevalence of frugivory among North American mammals (Martin et al. 1951, Halls 1977, Willson 1993), but few studies have addressed the ecological or evolutionary importance of carnivores as dispersal agents. For frugivores to have a positive effect on plant fitness, they must also be “legitimate”, “efficient”, and “effective” dispersers (Bustamente et al. 1992). Legitimate dispersers defecate seeds that are undamaged and capable of germinating, efficient dispersers defecate seeds in sites where they are likely to germinate and survive, and effective dispersers disseminate a large proportion of the seedlings that are recruited into the population.

Field studies have been conducted in Europe and South America on the ecological role of forest carnivores in fruit dispersal (e.g., Herrera 1989, Bustamente et al. 1992, Pigozzi 1992), but similar research has not been conducted in coniferous forests of western North America. However, a few studies have evaluated the legitimacy of forest carnivores as seed-dispersal agents in conifer forests. Black bears were considered to be legitimate fruit-dispersal agents in northeastern Minnesota because fruits were apparently swallowed whole and seeds were defecated intact (Rogers and Applegate 1983). The authors speculated that because many species of *Prunus* and *Pyrus* contain cyanogenetic glycosides, swallowing fruits whole may reduce the incidence of poisoning. Bears may also be relatively efficient dispersal agents, because germination rates of seeds from feces were higher than for seeds of uneaten fruits for all eight species studied, and significantly higher for five species. Thus, chemical or mechanical scarification in the gut of black bears enhanced the germination rate of fruit seeds. Six species of relatively small-seeded fruits from coniferous forests in southeast Alaska were fed to captive black bears, but only salmonberry (*Rubus spectabilis*) and elderberry (*Sambucus racemosa*) had significantly higher germination rates after gut passage than unpassed seeds (Traveset and Willson 1997). Because they are one of the few species capable of ingesting relatively large-seeded fruit and can travel up to 32 km per day (Rogers and Applegate 1983), black bears may be particularly important long-distance dispersal agents for large-seeded fruit.

Similar feeding trials involving salmonberry and two species of huckleberry (*Vaccinium alaskaense* and *V. ovalifolium*) were conducted on captive martens in southeast Alaska (Hickey et al. 1999). Passage through the gut of martens resulted in no difference in the germination rate for

V. ovalifolium compared to seeds taken from inside berries. Although gut passage decreased the germination rate for *V. alaskaense*, 41% were still viable. However, none of the salmonberry seeds fed to martens germinated. Thus, martens appear to be legitimate dispersers of huckleberry, but not salmonberry. In addition, movement models based on radio-telemetry data indicated that in four to five hours of travelling, martens are capable of transporting viable seeds in feces as far as 3.5 km.

Forest carnivores may also facilitate the long-distance dispersal of other propagules, such as mistletoe seeds and fungal spores. Dwarf mistletoe seeds are forcibly ejected from fruits in late summer or early fall (Hawksworth and Wiens 1996) and have been found on the fur of martens (Hawksworth et al. 1987). In the western U.S., martens and fishers often use witches' brooms caused by dwarf mistletoes as rest sites (Buskirk et al. 1987, Spencer 1987, Jones 1991, Seglund 1995, Parks and Bull 1997, Aubry and Raley 2001), and fishers have been documented using mistletoe brooms for maternal dens (Aubry and Raley 2001). Use of broom rest sites by both species occurs most often during the summer, probably because these sites are relatively exposed and provide poor protection from heat loss when ambient temperatures are low (Spencer 1987, Parks and Bull 1997, K. Aubry and C. Raley unpublished data). Because the timing of seed ejection coincides with the period when martens and fishers are most likely to use mistletoe brooms for rest and den sites, seeds may often be ejected onto their fur. Consequently, American martens and fishers may also facilitate the long-distance dispersal of dwarf mistletoes, due to their large spatial requirements and use of a variety of different structures within their home ranges for rest and den sites.

Forest carnivores may also disseminate fungal spores. Analysis of the stomach contents of eight fishers from northwestern California showed that the most important item by volume in the diet was the spores and tissues of the false truffle (*Rhizopogon* spp.; Grenfell and Fasenfest 1979). In a study conducted in southeastern California, spores from at least six genera of fungi were found to be ubiquitous in samples taken from 24 fisher scats; in 17 of the scats, fungal spores or tissue comprised 5% to 50% of the sample by volume (Zielinski et al. 1999). These findings indicate that fungal spores in fisher gastrointestinal tracts were not obtained solely by predation on northern flying squirrels, western red-backed voles (*Clethrionomys californicus*), or other mycophagous rodents. Fungi have not been reported in diets of the other forest carnivores considered here (Chapman and Feldhamer 1982), but have been reported

several times for the eastern spotted skunk (*Spilogale putorius*; Fogel and Trappe 1978).

Sporocarp tissues are fragile and may be unidentifiable in scats. In addition, most investigators do not examine carnivore scats or stomach contents for the presence of fungal spores. Thus, mycophagy by forest carnivores may be more common than is indicated by food habits studies reported in the literature. We do not know if fungal spores present in the gastrointestinal tracts of mycophagous rodents eaten by carnivores can be passed in a viable condition through carnivore digestive tracts. However, because hypogeous fungi have a highly co-evolved relationship with mycophagous small mammals and apparently rely on them for spore dispersal (Maser et al. 1978), it seems likely that spores would be well adapted to survive passage through the simpler gastrointestinal tracts of carnivores. Thus, either via mycophagy or predation on mycophagous small mammals, forest carnivores may also contribute to the long-distance dispersal of hypogeous fungi.

Forest carnivores as hosts for parasites

Mammals serve as hosts for a vast array of microparasites (e.g., bacteria, viruses, protozoans) and both internal and external macroparasites (e.g., helminths, arthropods; Scott 1988, Samuel et al. 2001). Taxonomists have only described a fraction of the species diversity represented by these organisms, however, and have only recently begun to study their influence on biodiversity and other ecosystem attributes (Windsor 1997, Brooks and Hoberg 2000). Infection by parasites can be relatively benign, as is the case for many species of macroparasites that rely on mammals to complete their life cycles, or it can cause diseases that result in morbidity or death. However, even relatively benign parasitic infections can affect host behavior, vigor, and reproductive output, which may in turn alter population demography, genetic diversity, and community interactions (Scott 1988). Because of their potential influence on the structure and functioning of ecosystems, and as a selective force in evolution, several ecologists have argued for an enhanced awareness of the role of parasites in the conservation of ecological diversity (May and Anderson 1983, Rózsa 1992, Windsor 1997, Murray et al. 1999, Brooks and Hoberg 2000). Although all tree-dwelling mammals perform this ecological function to some degree, we focused our discussion of this topic on forest carnivores because their ecological role as vertebrate predators also functions to complete or interrupt the life cycles of a variety of parasites.

The common macroparasites of forest carnivores have been well described (Samuel et al. 2001), but little effort has been made to understand the role of parasites in the ecology of forest carnivores or the functioning of forest ecosystems. In coniferous forests of the Cascade Range in Washington, American martens are commonly infected by the cestode *Taenia martis americana* (Hoberg et al. 1990), that is host-specific and cannot complete its life cycle in the absence of martens. In coastal areas of Washington, marten populations declined dramatically during the twentieth century and appear to have been extirpated in many areas (Marshall 1994, Zielinski et al. 2001). Consequently, the loss of martens from these areas probably also involved the extirpation of one or more of the parasite species they harbored. Martens are also reported to harbor the host-specific flea *Chaetopsylla floridensis* in the central Sierra Nevada in California (Zielinski 1984); thus, a similar scenario of co-extirpation is possible for ectoparasites of marten. Furthermore, because martens are carriers of the plague bacterium and suffer only brief clinical symptoms after infection (Marchette et al. 1962), they may also be involved in the epidemiology of plague. Because martens have much larger home ranges than the rodent prey species that serve as plague reservoirs, they may facilitate the transmission of infected fleas to uninfected rodent populations (Zielinski 1984).

Diseases do not appear to be an important source of mortality in black bears, American martens, or fishers. All are susceptible to trichinosis, however, and the latter two species carry other diseases such as toxoplasmosis, leptospirosis, and Aleutian disease (Rogers and Rogers 1976, Strickland et al. 1982a,b). Spotted skunks and raccoons are important vectors for rabies, histoplasmosis, and canine distemper, and raccoons are susceptible to several forms of encephalitis (Howard and Marsh 1982, Kaufmann 1982). However, the interrelationships among carnivores, parasites, and various ecosystem attributes remain largely unknown.

An assessment of key ecological functions of tree-dwelling mammals in the Pacific Northwest

Here, we assess the ecological functional roles played by native mammals (see Marcot and Aubry 2003) that are closely associated with trees in coniferous forests. For this analysis, we used the database of key ecological functions (KEFs) available for Washington and Oregon (O'Neil et al. 2001) to illustrate the array of KEFs provided by tree-dwelling mammals, and

to explore how management actions affecting their habitat elements can influence those functions. The term “key ecological function” refers to the major ecological roles played by each species. KEFs are hierarchically categorized according to the trophic and feeding roles of organisms, as well as their roles in nutrient cycling, and various kinds of organismal, disease, soil, wood structure, water, and vegetation relations (Marcot and Vander Heyden 2001). KEFs of species can influence habitat conditions and resources used by other species, thereby influencing the biodiversity and productivity of ecosystems. Thus, managers may wish to understand the effects of habitat management on KEFs. Many of these KEFs are well known, but their rates and specific effects on ecosystem diversity and productivity generally have not been quantified. Managers can view KEFs as testable management hypotheses about how tree-dwelling mammals may influence a particular ecosystem.

KEFs of mammals associated with specific vertical tree structures

Among the nine forested habitat types that occur in Washington and Oregon, 27 mammal species are associated with vertical tree structures (Table 12.1). Most of these species occur in forests west of the crest of the Cascade Range, and fewer occur in western juniper and mountain mahogany woodlands and in lodgepole pine forest and woodlands (Fig. 12.1). Species composition varies among forest types, and even the low-richness types provide unique habitats for some species.

Collectively, the 27 species participate in 60 categories of KEFs; because tallies of KEFs include both categories and subcategories, there is some minor duplication in the counts. These KEFs in turn extend well beyond the immediate vertical tree structures with which the species are associated. As examples: of the 27 species, 11 species of bats and one carnivore may decrease insect populations through insectivory; one squirrel and two carnivores excavate burrows and create runways that can be used by other species; five rodents and five carnivores help disperse seeds, spores, plants, or animals, including dispersal of fungi, lichens, and fruits; six rodents create nesting structures that can be used by other species; two rodents churn soil by digging, potentially improving soil structure and aeration; and other functions.

Nine habitat elements pertaining to vertical tree structures provide part of the habitat requirements for these 27 species, and thus support the array of KEFs performed by those species (Fig. 12.2). The four vertical

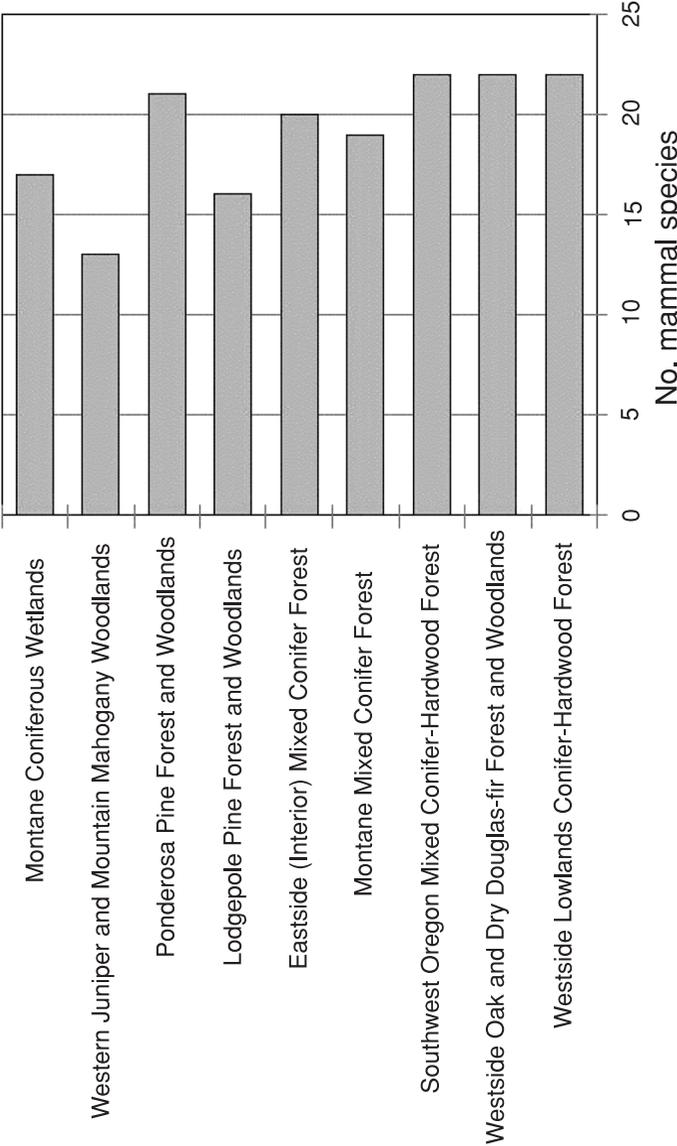


Fig. 12.1. Number of mammal species associated with large tree structures in the nine forested wildlife habitat types occurring in Washington and Oregon (Chappell et al. 2001).

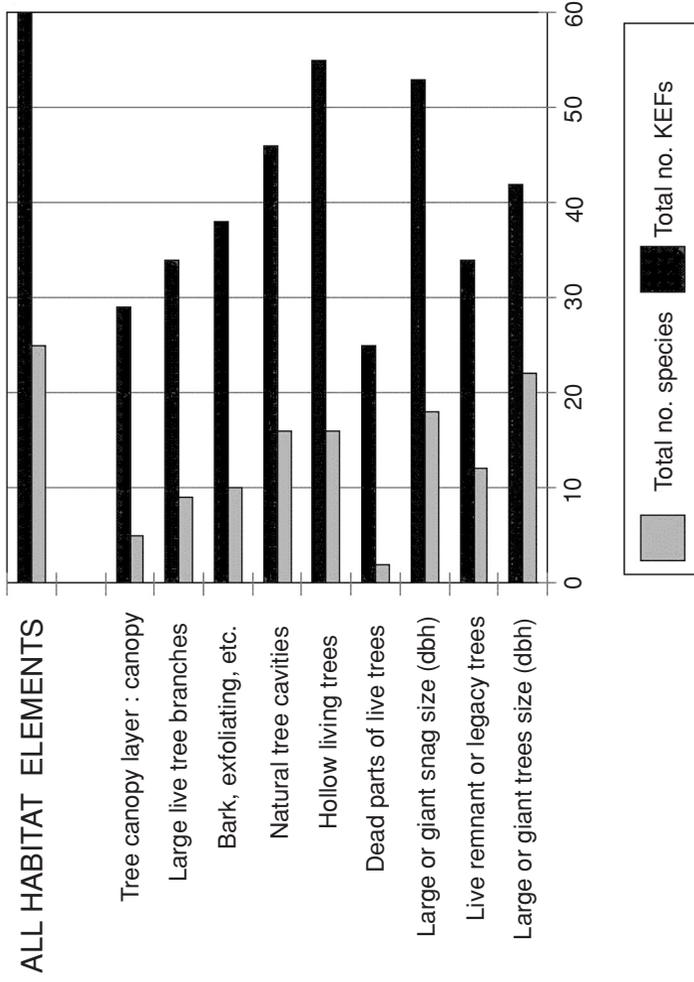


Fig. 12.2. Number of mammal species associated with vertical tree structure habitat elements (vertical axis) and the number of categories of key ecological functions (KEFs) they perform collectively in forests of Washington and Oregon.

tree structures that provide for the greatest number of these 27 species and their associated KEF categories are hollow living trees, large or giant snags, natural tree cavities, and large or giant live trees. However, even those structural elements, such as the dead parts of live trees, that provide for relatively few of these species and KEFs nonetheless make unique contributions to several species, and may play important roles in ecosystem function.

To managers, this means that providing vertical tree structures (as listed in Fig. 12.2) within each of these forest types not only provides some of the habitat needs of these species, but also helps contribute to the “functional web” of their ecological roles within ecosystems. The specific array of KEFs and associated species varies by type of vertical tree structures and forest habitats. Thus, all forest types are necessary to provide the full, collective array of these species and their KEFs. The specific rate of each ecological function, however, and the quantitative influence on ecosystem productivity, are essentially unstudied. Our evaluation provides a qualitative starting point by which to test functional roles as management hypotheses.

Information and research needs

Our review shows there is empirical support for the ecological roles we have hypothesized for tree-dwelling mammals in western coniferous forests. However, research that quantifies how and to what extent this group of mammals influences the composition, structure, or functioning of ecosystems is generally lacking. For example, we know that bats consume large numbers of nocturnal insects, but we do not know if their foraging activities regulate the size of nocturnal insect populations. Similarly, we know that arboreal rodents and forest carnivores transport and probably aid in the long-distance dispersal of fungal spores and dwarf mistletoe seeds, but we do not know whether ectomycorrhizal fungi would be unable to inoculate areas of new regeneration, or if mistletoe infections would be reduced in mature forests, in the absence of tree-dwelling mammals. Field studies designed to answer such questions will be challenging, but are essential for understanding the ecological roles that tree-dwelling mammals play in coniferous forest ecosystems.

Comparing similar ecosystems with and without a given species may be the most useful approach to understanding the ecological importance of that species, even though such studies may suffer from inadequate

replication or controls (Estes 1996). Manipulative experiments involving the removal of tree-dwelling mammals from forested ecosystems are neither feasible nor socially acceptable. However, local extirpations and subsequent re-introduction efforts provide unique opportunities to study the ecological importance of tree-dwelling mammals. For example, both martens and fishers were extirpated from large portions of their former range in the Pacific states during the last century (Zielinski et al. 1995, Aubry et al. 1996, Zielinski et al. 2001). In response to these population declines, the Washington Department of Fish and Wildlife has begun to plan the re-introduction of fishers to Washington state, and re-introductions may also occur in portions of Oregon and California where fishers no longer occur. Thus, opportunities currently exist to compare ecosystem processes in western coniferous forests with and without these species, and to conduct such studies before and after re-introductions. Empirical evaluation of the ecological roles we have hypothesized for tree-dwelling mammals would also increase our understanding of the functioning of coniferous forest ecosystems and provide a much stronger scientific basis for evaluating forest management and conservation alternatives.

Summary

Despite the scarcity of empirical evidence, we hypothesize that bats have an important influence on ecosystem function in western coniferous forests because of their abundance and the specialized ecological niches they occupy. Bats serve as prey for aerial predators and as agents of nutrient transport, but we suspect that these functions influence ecosystem processes at relatively small spatial scales, such as at roosting and foraging sites. We predict that the most important ecological role performed by bats is their influence on nocturnal insect populations.

With the exception of extensive work on the role of arboreal rodents in the dissemination of ectomycorrhizal fungi, few studies have examined the ecological influence of arboreal rodents in western coniferous forests. By dispersing these specialized fungi, arboreal rodents help sustain productivity of both forests and forest commodities in western coniferous forests. In addition, arboreal rodents are important prey for both avian and mammalian predators, and some predator populations may be strongly influenced by the diversity and abundance of arboreal rodents.

In western coniferous forests, tree-dwelling carnivores may be important agents for long-distance dispersal of propagules, and may contribute

to the maintenance of biodiversity by serving as hosts for a variety of parasites. With several exceptions, forest carnivores do not appear to exert strong influences on populations of competitors or prey in western coniferous forests. However, Terborgh (1988) argued that top predators are primarily responsible for the stability and extraordinary diversity of plants and animals in pristine tropical forests. He reasoned that this profound influence on ecosystem structure resulted from the propagation of perturbations through multiple trophic levels in the ecosystem. Thus, effects are felt even in organisms that are far removed, both geographically and taxonomically, from the predator and its prey. Whether forest carnivores exert a similarly strong influence on ecosystem structure in western coniferous forests is unknown.

We have argued that managing forests solely for the persistence of a few key vertebrate species or target vegetative conditions is an overly simplistic approach to forest management, and one that is unlikely to provide for long-term ecosystem sustainability. We believe that resource managers can improve the outcome of management decisions in western coniferous forests by considering the ecological roles that mammals play and evaluating the functional webs to which they contribute. By comparing the array of ecological functions that are predicted to occur under a set of alternative management strategies, managers can select the alternative that will be most likely to provide for long-term ecosystem integrity.

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