7

Small and mid-sized carnivores

The small and mid-sized carnivores (Carnivora), or mesocarnivores of western forests comprise 16 species (coyote (*Canis latrans*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), ringtail (*Bassariscus astutus*), raccoon (*Procyon lotor*), marten (*Martes americana*), fisher (*M. pennanti*), ermine (*Mustela erminea*), long-tailed weasel (*M. frenata*), mink (*M. vison*), wolverine (*Gulo gulo*), northern river otter (*Lontra canadensis*), western spotted skunk (*Spilogale gracilis*), striped skunk (*Mephitis mephitis*), Canadian lynx (*Lynx canadensis*), and bobcat (*Lynx rufus*)). The term "forest carnivores" denotes a smaller group of four species – the marten, fisher, lynx, and wolverine – and is only marginally descriptive, inasmuch as it excludes many carnivores that live in forests, and includes the wolverine, which can thrive in the complete absence of trees. The species we consider here represent four (or five (Dragoo and Honeycutt 1997)) taxonomic families and are characterized by adult body weights typically <20 kg. Other mesocarnivores, including the kit fox (*Vulpes macrotis*), swift fox (*V. velox*), least weasel (*Mustela nivalis*), black-footed ferret (*M. nigripes*), and badger (*Taxidea taxus*), occur in the West, occupy habitats near forest edges, and may be conservation concerns. However, they are plains or grassland specialists or, in the case of the least weasel, very poorly known, and cannot be characterized in terms of their needs for forest attributes. So, they are not treated here.

Our understanding of the ecology of carnivores in western coniferous forests varies markedly. American martens have been studied in the West in relation to habitats (at various scales), diets, populations, energetic

physiology, and reproduction. On some topics, multiple studies have been published. By contrast, ringtails in the north temperate zone are known from only a few studies, and even descriptive habitat use of forests is weakly documented. Perhaps surprisingly, some common species (e.g., raccoon) have received only the most cursory study in relation to habitats in the West. Therefore, we refer to midwestern and eastern studies, recognizing that those results may have limited applicability to habitats in the West.

Perhaps unavoidably, knowledge of habitat requirements of forest obligates is clearer and more specific than for habitat generalists. The latter tend not to receive detailed habitat study because they are not interesting models of habitat selection, and require large sample sizes to even detect selection. Raccoons and ringtails, for example, both rest in cavities in broad-leaved trees and snags, but links between both species and structural or successional stages of upland coniferous forest are unclear, and possibly weak.

Species accounts

We group the mesocarnivores into four habitat strata: habitat generalists, forest specialists, riparian associates, and semi-aquatic species, following the classification of Cooperrider et al. (1999). Habitat generalists occur in a wide range of forested and non-forested habitats, forest specialists are limited to forests and habitats nearby, riparian associates occur primarily in special habitats around water bodies or saturated soils, and semi-aquatic species forage or travel mostly in water, but perform other life functions on land. All species considered here have broad geographical ranges; for example the long-tailed weasel from northern British Columbia to Bolivia. And, all but two species (ringtail and wolverine) have broad distributions or sibling species in eastern North America.

Habitat generalists

Coyote

The coyote is arguably the most cosmopolitan and adaptable mesocarnivore of western North America, having expanded its geographical range and increased its abundance, including in the northwest, over the past 50–100 years (Buskirk et al. 2000*a*). Coyotes are best adapted to non-forested habitats, having been called brush wolves (as contrasted with "timber wolves" (*Canis lupus*)) by early explorers. They have expanded into formerly inaccessible continuous forest as a result of fragmentation,

particularly road building, land conversion, and timber harvesting. Today, coyotes are common or abundant in a wide range of forested ecosystems throughout the West, including the 3030- to 3333-m elevation zone in Colorado (G. Byrne 1998 unpublished, cited in Buskirk et al. 2000*a*). Coyotes feed on a wide range of items in the West, including mammals, birds, fruits, and invertebrates. Two factors, one abiotic and the other biotic, can be severely limiting to coyotes. Deep, soft snow can limit the distribution of coyotes (Todd et al. 1981), because of their presumably high energetic costs while walking through deep snow, as inferred from foot loadings (Buskirk et al. 2000*a*). So, areas of the West with deep, soft snow and no avenues for access should have fewer coyotes than elsewhere, although this hypothesis has not been rigorously tested. The presence of sympatric larger-bodied carnivores, particularly wolves, is an important biotic limiting factor to coyotes. Coyotes alter their behaviors, exhibit reduced densities, or become locally extinct in the presence of wolves (reviewed by Buskirk 1999, Buskirk et al. 2000*a*). Where they are common, on the other hand, coyotes have pivotal community functions because of their predation on and competition with a wide range of smaller carnivores (Sovada et al. 1995, Henke and Bryant 1999). Coyotes are variously credited with suppressing populations of native and non-native mesocarnivores, thereby protecting smaller vertebrate populations (Crooks and Soulé 1999) or threatening native vertebrates (White and Garrott 1997), their perceived value being context- and taxon-specific. But there is increasing recognition that they are important factors in the conservation of mesocarnivores, small birds, and small mammals (Ralls and White 1995, O'Donoghue et al. 1998, Rogers and Caro 1998) by nature of being opportunistic predators, and the largest predators remaining in many areas of the West. Coyotes appear to be benefited by forest-management practices that create openings in previously extensive forests via clearcutting or road building, and may benefit from activities that create trails in deep, soft snow. Foods made available by humans, including refuse, livestock, some crops, and pets, can be important to coyotes. Perhaps most importantly, programs to restore the wolf to its former distribution in the West have important implications for the distribution and abundance of coyotes.

Red fox

With the historical reduction in the distribution of wolves, the red fox now has the widest global distribution of any mammal other than humans and our associated commensal species (Voigt 1987). The Holocene and Recent

zoogeography of the red fox in the West is exceedingly complex, involving indigenous and introduced forms (Aubry 1984), some expanding and others shrinking their distributions, presumably in response to human-caused changes. In coniferous forests of the West, the red fox occurs in at least three forms: in Canada and Alaska, native foxes are assigned to three to four subspecies, and occur at various elevations and in various habitats. In the western contiguous United States and southwestern British Columbia, however, foxes include those in primarily lowland habitats, which were introduced from the eastern United States (*V. v. fulva*), and three indigenous subspecies (*V. v. macroura* of the Rocky Mountains, *V. v. cascadensis* of the Cascades, and *V. v. necator* of the Sierra Nevada). The introduced, low-elevation form has expanded its distribution dramatically since the early 1900's (Grinnell et al. 1937) into areas that previously did not have red foxes, whereas the high elevation form has declined in distribution and abundance and represents a conservation concern (Schempf and White 1977, Aubry 1984).

The high-elevation form has a unique evolutionary history; presumptively representing vicariant post-glacial relicts. Its restriction to high elevation, especially alpine habitats (Grinnell et al. 1937, Aubry 1983, Crabtree 1993), seems at odds with the otherwise broad tolerances of the species as suggested by its vast distribution and habitat generalization within the northern part of the New World range. The lowland temperate western red foxes, escaped from fur farms, have expanded their distribution in recent decades into grasslands and coastal marshes (Lewis et al. 1995), as well as interior deserts. Burrows in soil or rock piles are typically used as natal dens. Both introduced and indigenous forms are dietary generalists, feeding on rodents, lagomorphs, insects, fruits, carrion, and birds (Voigt 1987).

The Cascade and Sierra Nevada red fox populations are at the greatest risk of extinction; both appear to be small and in decline (Schempf and White 1977, Aubry 1983). The Sierra Nevada red fox has been considered extremely sensitive to the presence of humans (Grinnell et al. 1937) so that increased recreation within its range could be problematic. The expanding range of the lowland, introduced, red fox poses a risk to the native form via genetic introgression (Aubry 1984, Lewis et al. 1995), which presumably was minimized in the past by densely forested areas that separated them (Aubry 1983). In Yellowstone, the high-elevation red fox found on the Beartooth Plateau has been hypothesized to be negatively affected by coyotes (Buskirk 1999).

Gray fox

The gray fox prefers brushy vegetation in broken terrain and uses woodland habitat more frequently than does the red fox (Samuel and Nelson 1982). Gray foxes are unique among North American canids in their strong tree-climbing ability. In California, riparian areas and old-field habitats were used more frequently than expected (Fuller 1978) and in Utah brushy meadows were favored (Trapp 1978). Natal dens are found in brush piles, rocky outcrops, and hollow trees (Trapp and Hallberg 1975). Lagomorphs, rodents, and small birds are the primary prey, but fruit can dominate the diet in summer and fall (Wilcomb 1948, Trapp 1978). Although trapped for fur in most western states, their fur is not highly prized. They associate with human development to some extent (Riley 1999), but high-density residential development (Harrison 1997) and fragmentation of forested lands (Rosenberg and Raphael 1986) each reduce habitat for gray foxes. Continued regulated trapping should provide data to allow the assessment of status and distribution.

Ermine

The distribution of the ermine overlaps extensively with the larger long-tailed weasel and may be limited by interference competition between the two species (Simms 1979). Ermines occur primarily where voles are common, typically meadows and grasslands in temperate forests. However, this weasel is frequently found in forests and shrub habitats (Hooven and Black 1976, Gilbert and Allwine 1991), unlike in the East (Simms 1979, Verts and Carraway 1998). In the North, this is the only common forest weasel. Grass nests constructed by voles in the winter are usurped by ermines for resting sites (Fitzgerald 1977). Because of its smaller size, the ermine, more than the long-tailed weasel, specializes on voles and mice (Simms 1979), captures them in subnivean spaces (Fitzgerald 1977, Simms 1979) and uses mouse nests for shelter.

Because they associate with meadows in forests, ermines probably are vulnerable to the effects of livestock grazing on vegetation; small mammal prey may be secondarily affected. Encroachment of trees into meadows, due to fire suppression or changes in climate, may also reduce weasel habitat.

Long-tailed weasel

The long-tailed weasel is the largest weasel of the West, and may occur in any habitat, including mature forests, recently logged areas, meadows, and tundra (Simms 1979, Svendsen 1982, Fagerstone 1987). They are

common in meadows when vole populations are high and use the nests of their microtine prey during the winter (Fitzgerald 1977). They are less subnivean than ermines, presumably being more constrained by their larger bodies (Simms 1979); the northern limit of their distribution may be limited by snow. Long-tailed weasels are primarily carnivorous, consuming a wider range of prey than ermines, but relying predominantly on *Microtus, Clethrionomys, Peromyscus,* and *Tamias* (Hamilton 1933, Quick 1951). Insofar as they associate with grassland and meadow habitat within forests, long-tailed weasels may be vulnerable to the loss of herbaceous and shrub cover resulting from grazing. Encroachment of trees into meadows, due to fire suppression or changes in climate, may also eliminate some long-tailed weasel habitat.

Wolverine

The wolverine was historically distributed throughout most of Alaska and Canada, southward through the montane West to Utah, Colorado, and California (Banci 1994). Wolverines are now uncommon or rare in the contiguous United States (Wilson 1982, Banci 1994), where the present distribution comprises several peninsular or island extensions of the northern core (Hash 1987, Banci 1994). Wolverines occur in north-central Idaho and northwestern Montana (Banci 1994, Maj and Garton 1994), and may persist in parts of Oregon and Washington (Edelmann and Copeland 1999), but are exceedingly rare in or absent from California and Colorado. Wolverines are generally restricted throughout their temperate western range to boreal forests, tundra, and high-elevation grasslands (Banci 1994). Wolverine habitat, however, is less defined by vegetation types than by where adequate year-round supplies of food occur in extensive wilderness areas. Preferences for particular habitats have been attributed largely to differences in the availability of food (Gardner 1985, Banci 1987), but the availability of coarse woody debris (dead woody material >10 cm diameter: CWD) and rocky areas for resting, rendezvous and denning sites may be critical (Banci 1994). Natal dens tend to occur in rock crevices in talus slopes of high-elevation cirque basins, piles of CWD, and snow tunnels (Hash 1987, Magoun and Copeland 1998), but other protected structures have been reported to be used as well (Grinnell et al. 1937). The diet is composed primarily of the carrion of large mammals, particularly ungulates (Banci 1994). In coastal environments, however, the carrion of marine mammals and salmon is commonly eaten (Banci 1987). In the North, wolverines are closely associated with caribou (*Rangifer tarandus*)

(Banci 1987, 1994) and may follow caribou herds. Small mammals (e.g., ground squirrels (*Spermophilus* spp.), marmots (*Marmota* spp.), snowshoe hares (*Lepus americana*), porcupines (*Erethizon dorsatum*)) and birds (e.g., ptarmigan (*Lagopus* spp.)) are important prey only when the carrion of larger mammals is unavailable (Banci 1987, 1994).

Wolverines are trapped in Canada, Alaska and Montana (Banci 1994) and caution is required to assure that harvests are sustainable. Recent harvest levels in Alaska (10% of fall populations) have exceeded estimates of sustainable levels (Gardner et al. 1993 cited in Banci 1994). The importance of timber harvest to wolverines is not clear; canopy cover and CWD have been reported to be important (Hornocker and Hash 1981, Banci 1994, Copeland 1996). However, most wolverine habitat occurs away from commercial timber harvest so areas of conflict may be quite localized. The greatest threat to populations of wolverines, similar to that for other low-density carnivores, is the fragmentation of their habitat and populations by human structures and activities. Wolverine populations at the southernmost margin of the range may require episodic dispersive inputs to maintain viability, and wilderness habitat corridors may be important for such movements. The frequency and direction of such movements is not known. Wolverines are extremely intolerant of the presence of humans, and the distribution of wolverines in the West coincides largely with the regions of lowest human density (Hornocker and Hash 1981, Banci 1994, Carroll et al. 2001). Perhaps more so than for other species considered here, the mechanism by which human activity excludes wolverines is not known.

Western spotted skunk

The western spotted skunk is parapatric with its eastern counterpart, *S. putorius*, in Colorado and New Mexico. Spotted skunks occur in a variety of habitat types across their range in western North America. In particular regions, however, they are strongly associated with specific cover types and habitat elements. In eastern Oregon, they commonly associate with canyons, cliffs, lava fields, and arid valleys (Bailey 1936), whereas in coastal Oregon they are common in dense forest stands with old-growth elements and dense shrub cover (Carey and Kershner 1997). In California, various subspecies seem to associate with highly varied elements in landscapes from sea level to >2000 m (Orr 1943), but typically with dry rocky uplands characterized by shrubs and little forest cover (Grinnell et al. 1937). Resting occurs in log and tree cavities, rock crevices, wood rat

(*Neotoma* sp.) nests, mountain beaver (*Aplodontia rufa*) tunnels and human structures (Grinnell et al. 1937, Maser et al. 1981, Crooks and Van Vuren 1995). They are excellent climbers. The diet has been described only for the Channel Islands spotted skunk (*S. g. amphiala*), which feeds on deer mice (*Peromyscus maniculatus*), insects, and lizards (Crooks and Van Vuren 1995). The congeneric *S. putorius* feeds primarily on small mammals in winter and arthropods in summer (Crabb 1941). Spotted skunks are trapped for their fur in some western states and provinces, but most animals likely are caught incidental to more valuable furbearers and this does not result in measurable population-level losses (Verts and Carraway 1998). A larger cause of deaths is encounters with humans and their pets around human habitations (Crabb 1948, Verts and Carraway 1998). The incidence of rabies in spotted skunks does not approach that in striped skunks (Krebs et al. 1995*a*), but the perceived association between all skunks and rabies accounts for much unwarranted persecution of spotted skunks.

Striped skunk

Although occurring in forests and forest edges, the striped skunk is mostly a species of open habitats. In coastal regions it can occur in dune, prairie, and meadow communities as well as in early-seral forests (Maser et al. 1981). In interior regions striped skunks are common in valleys with mixtures of pasture, crops, and brush and also in woodlands and open fields broken by wooded ravines and rocky outcrops (Wade-Smith and Verts 1982). They associate closely with human structures in suburban and urban settings (Godin 1982). Typical of lower elevations in California, they seldom occur above 1500 m (Grinnell et al. 1937). They forage on the ground, rarely climb trees (Godin 1982), and may dig shallow burrows for resting sites, but prefer rock crevices, burrows of other species, and holes within or beneath logs (Godin 1982). Striped skunks primarily eat insects and small mammals (Grinnell et al. 1937, Verts 1967). They are still commonly trapped for their skins, but pelt values are low and trapping has not been considered a threat to populations (Godin 1982). Reported rates of occurrence of rabies in striped skunks are among the highest reported for wild or domestic mammals, which contributes to their persecution in many areas.

Bobcat

Within their range, bobcats occur in a wide range of vegetation types, including coniferous forests, marshy hardwood forests, high-elevation shrublands, and deserts. They associate with dense physical structure in

the form of shrubs and woody debris of various sizes, and exhibit no particular tie to late-successional stages. Indeed, bobcats in the Southeast have been shown to select for early seres (Miller 1980), and those in Oklahoma heavily used forested sites <10 years after clear-cutting (Rolley and Warde 1985). Bobcats also show some preference for sites with rock ledges and outcrops, in part because of the shelter that such features provide (Zezulak and Schwab 1979). Seasonal shifts in habitat have been described (Rolley 1987); at the northern edge of the range these include winter shifts toward habitats with lower snow depths (McCord 1974), reflecting the heavy foot-loadings for the species (Buskirk et al. 2000*a*). The importance of trees and particularly CWD to bobcats is apparently low relative to other mesocarnivores. Bobcats in central Idaho were found to prefer open over timbered habitats (Koehler and Hornocker 1991), and no evidence suggests strong ties to late-successional forests in the West.

Foods of bobcats are almost entirely mammals and birds; in the West the most common prey are lagomorphs (Rolley 1987) and rodents (Riley 1999). A general reduction in the distribution of bobcats in the urban East apparently has not been reflected in the West. The principal conservation concerns for bobcats in the West have tended to be related to trapping mortality. Yearly survival rates in heavily trapped populations have been around 0.6 (Rolley 1987), but as low as 0.19 (Fuller et al. 1985). With the decline of the trapping industry for the past 15 years, however, concerns about trapping mortality have dwindled correspondingly. As explained below, bobcats are presumably susceptible to competitive interactions with larger carnivores. No clear approaches to habitat management that would favor bobcats are known for the West. Either the species is insensitive to most common forestry practices, or our knowledge base is too weak to support any salient inferences.

Forest specialists

Marten

The marten is a specialist of coniferous forests of the boreal zone and southern peninsular extensions (Hagmeier 1956, Gibilisco 1994). Martens prefer mesic, conifer-dominated forests with abundant physical structure near the ground and avoid areas lacking overhead cover, particularly in winter (Buskirk and Powell 1994). In some areas of Alaska and northwestern Canada, martens use early seres following burns (Paragi et al. 1996), so that downed tree boles combined with dense herbaceous vegetation can address the need for cover. The avoidance of areas lacking sufficient cover

has been called a "psychological need" (Hawley and Newby 1957), and presumably relates to vulnerability to attack by other carnivores and raptors. During the winter, structures near the ground provide access to subnivean spaces for resting and foraging (Buskirk and Ruggiero 1994). Throughout the year martens use cavities in large-diameter live and dead trees as resting sites (Buskirk and Ruggiero 1994) and as natal dens (Ruggiero et al. 1998). In the West, martens are strongly associated with old-growth coniferous forests, but they occur in earlier seres that include remnants of old-growth forest, for example stumps and logs (Baker 1992). Martens generally do not occur in landscapes where more than one-third of the landscape is in openings (Chapin et al. 1998, Hargis et al. 1999, Payer 1999, Potvin et al. 2000). Minta et al. (1999) hypothesized that martens are most selective at the finest scales (scale of foraging and resting sites) and coarsest scales (population selection of landscape types), but less selective at intermediate scales (patch and home range). At regional scales, the amount of habitat and its distance from nearby source populations influence the occurrence of martens on insular mountain ranges in the interior West (Wisz 1999).

Martens eat primarily rodents, lagomorphs, birds, fruit seasonally, and carrion opportunistically (Martin 1994). Voles are the primary prey, particularly in the North (Martin 1994), and *Microtus* spp. and other large-bodied species appear to be preferred because they are consumed in excess of their availability (Weckwerth and Hawley 1962, Buskirk and MacDonald 1984). Larger prey (e.g., lagomorphs, tree squirrels) constitute more of the winter than summer diet (Zielinski et al. 1983, Thompson 1986, 1994). Martens have important ecological relationships with red squirrels (*Tamiasciurus hudsonicus*) and Douglas squirrels (*T. douglasii*) (Buskirk 1984, Corn and Raphael 1992, Sherburne and Bissonette 1993) and in some studies these species compose a significant part of the diet (Martin 1994).

Martens are trapped for their fur in several states and most Canadian provinces (Buskirk and Ruggiero 1994), but are fully protected in a growing number of jurisdictions. Populations are easily over-trapped, which led partly to the reduced distribution and abundances through the early 1900's, including from much of the Coast Ranges of California and Oregon (Zielinski et al. 2001). Even light trapping pressure can inflict high mortality (Schneider 1997); limiting the number of licensed trappers and setting quotas are common practices (Strickland et al. 1982*a*, *b*). Timber harvest, especially clear-cutting of mature and old-growth forests, also affects martens negatively (Buskirk and Ruggiero 1994, Thompson and Harestad

1994, Hargis et al. 1999, Payer 1999). Logging results in the direct loss of resting and foraging habitat and increases energetic costs due to avoidance of openings and the maintenance of larger home ranges (Potvin et al. 2000). Partial harvest (thinning) results in stands that are avoided in winter but not summer (Fuller 1999). In Maine, reproduction is higher and mortality from trapping is lower in unharvested forests than in commercial forests (Payer 1999). Trapping mortality also is additive to natural mortality in commercial forests (Payer 1999). Responses of martens to habitat change in general and to landscape fragmentation in particular are not linear (Hargis et al. 1999). Martens exhibit threshold responses to the extent of forest harvesting, and population declines beyond the threshold may be abrupt (Bissonette et al. 1997). Grazing by livestock may affect martens via altering habitat for voles adjacent to resting habitat. Roads are a source of mortality and negatively affect the distribution of marten activity (Robitaille and Aubry 2000).

Fisher

Fishers occur in mesic, conifer-dominated forests of the boreal zone and southern peninsular extensions (Hagmeier 1956, Gibilisco 1994). Primary habitat is dense coniferous forest, usually with a deciduous component and abundant physical structure near the ground (Buskirk and Powell 1994, Powell and Zielinski 1994). Fishers use cavities in large-diameter trees, snags, and logs as daily resting sites (Powell and Zielinski 1994) and as natal dens (Roy 1991, Aubry et al. 1997). Mid-elevation old-growth forests provide needed habitat elements, but fishers travel through, and in some areas occupy, home ranges in regenerating forests that have dense cover and a sufficient number of large structures, especially hardwood boles, for resting (Klug 1996). In more xeric regions, or where logging has removed upland forest cover, riparian zones provide important habitat (Roy 1991, Heinemeyer 1993, Seglund 1995). Fishers avoid regions with deep, soft snow, because of their heavy foot loadings (Krohn et al. 1997). Kelly (1977) and Carroll et al. (1999*a*) found that habitat selection appeared to be dominated by factors acting at the scale of the home range and above, contrary to the results of Weir and Harestad (1997). In northwestern California, landscape-level indices of canopy closure, size of trees, and percentage conifer interact with regional climatic and geographical variables to explain the occurrence of fishers (Carroll et al. 1999*a*). Regional habitat of fishers in the Rocky Mountains, modeled using remotely sensed variables, is best described by a combination of precipitation, elevation,

"wetness," "greenness," road density, canopy closure, and variation in tree size (Carroll et al. 2001). This confirms the general notion that fishers are strongly associated with productive, low- to mid-elevation forests.

Fishers eat snowshoe hares and porcupines over much of their range (Powell 1993, Martin 1994). Where snowshoe hares and porcupines are uncommon, the diets of fishers are more diverse, including significant quantities of other mammals, reptiles, fruits, insects, and fungi (Zielinski et al. 1999). Two California studies (Grenfell and Fasenfest 1979, Zielinski et al. 1999) showed that fishers eat fruiting bodies of false truffles (*Rhizopogon* spp.).

Fishers are protected from trapping over most of the western states, but are legally trapped throughout Canada and the north-central states (Powell and Zielinski 1994). They are easily over-trapped, even in a short, early trapping season, especially when trapping pressure is heavy (Powell 1979). Fishers are also vulnerable to incidental capture in traps set for other species (Lewis and Zielinski 1996). Where trapping is heavy, limiting the number of licensed trappers and setting quotas based on demographic characteristics of the harvest is necessary (Strickland et al. 1982*a*, Strickland 1994). In the West, fishers avoid recently clear-cut areas and are almost always associated with old stands or old remnant structures in regenerating stands (Buck et al. 1994, Jones and Garton 1994). Their need for continuous forest cover (Rosenberg and Raphael 1986, Carroll et al. 1999*a*) may account for their loss from areas that are intensely managed for timber. Regional persistence seems to reflect the sizes and arrangements of suitable habitat patches; as habitat becomes fragmented, the distribution collapses to include only the largest patches of source habitat (Carroll et al. 2001). All study animals found dead ($n = 7$) in one northwestern California study ($n = 21$) were recovered from clear-cuts, areas lacking overhead cover, or hardwood-dominated stands (Buck et al. 1994), showing that mortality was highest in areas found to be avoided in use-availability analyses. Where sympatric in the West, fishers generally occur at lower elevations than martens (Grinnell et al. 1937, Zielinski et al. 1997, Verts and Carraway 1998), and therefore may encounter roads more frequently.

Canadian lynx

Lynx are now much reduced in distribution and abundance (McKelvey et al. 2000*a*) and contiguous US populations were listed under the

Endangered Species Act in 2000. In the West, lynx are specialists of mesic coniferous forests of the boreal zone and southern peninsular extensions (McKelvey et al. 2000*a*). Lynx require habitat that will produce sufficient densities of their obligatory prey, snowshoe hares and red squirrels (Aubry et al. 2000). These species, in turn, require high densities of small-diameter woody stems and cone-bearing ages of conifers, respectively. The plant species, successional stages, and moisture regimes that produce these conditions and adequate prey densities are region-specific (Buskirk et al. 2000*b*). In the North, where populations are strongly cyclic, high densities of small-diameter woody stems tend to occur in early seres, before the closed-canopy stage of stand development. Therefore, in the North early successional stages with dense small woody stems are important to lynx; the role of late successional forests is unclear. However, red squirrels are important prey during periods of hare scarcity (Mowat et al. 2000); therefore, coniferous forest with high densities of red squirrels may be important for the survival of lynx between peaks in hare populations.

In the western contiguous US, snowshoe hare population cycles have small or imperceptible amplitudes (Hodges 2000) and population densities tend to be similar to those during population troughs in the North. Red squirrels tend to be more important prey in the southern part of the distribution, commonly representing 25% to 35% of prey items (Aubry et al. 2000). Here, dense woody stems are absent from some early seres; dry soils during summer can slow regeneration, and dense shrubs are uncommon in early seres, except on moist sites. In such dry landscapes, high-quality lynx habitat may be limited to moist sites: north-facing slopes, riparian zones, and late-successional stands with shaded understories. Cone-bearing ages of conifers important to red squirrels may be more important for lynx in the southern part of the range than in the North, because of the presumably greater importance of red squirrels in the diet.

Although habitat quality for lynx tends to be evaluated in terms of habitat for prey, other factors, including openings in which snowshoe hares can be caught and denning habitat, are important to lynx. Denning sites have tended to be in areas with abundant CWD (Mowat et al. 2000). Management of forests for lynx must be based on site-specific conditions and address all of the life needs of the lynx, including those for reproduction.

Riparian associates

Raccoon

Raccoons occur in a fairly wide range of habitats throughout the West, but to a greater degree than other procyonids, near water. They are uncommon in upland forests and woodlands, and above 2500 m, which effectively excludes them from coniferous forests of the interior West. However, their distribution across habitats, including deserts and interior mountains, and abundance have increased in the last 70 years, abundance by as much as an estimated factor of 20 (Sanderson 1987). Human-caused environmental changes have been credited with contributing to that increase (Gehrt 2003). As a result, raccoons are seldom identified as a conservation concern in forest management. More commonly they are considered pests or, where introduced, threats to indigenous taxa (Hartman and Eastman 1999).

Habitats of raccoons in western forests have been studied little. Riparian forest structure can be important for resting sites, because raccoons rest in tree cavities, and can attain body sizes large enough to require large cavities, and therefore large trees. Over most of the range of raccoons, resting trees have tended to be broad-leaved species. Stuewer (1943) found that resting cavities in Michigan were 3–12 m above ground, with average dimensions 29 cm × 36 cm. Where large trees with hollow cavities are unavailable, raccoons rest in holes in the ground, brush piles, and human structures, but may be more vulnerable to coyotes and other predators when resting near the ground. Raccoons eat an exceptionally wide range of foods (Gehrt 2003), with plant foods tending to predominate at most times. Hard mast is important where available, and corn is important where it is grown. Animal foods tend to be most important in late winter and early spring, and include invertebrates and fish (Tyson 1950), muskrats (Dorney 1954), and crippled waterfowl (Yeager and Elder 1945). In urban and suburban settings, human food sources can be important or dominant (Gehrt 2003). The proximity of foraging areas to resting and denning cover may be crucial, but has not been investigated in the West. The primary mortality causes for raccoons over most of their range are human-related, especially trapping and vehicle collisions (Chamberlain et al. 1999, Gehrt 2003).

Ringtail

The smallest of the north-temperate procyonids, ringtails occur in a wide range of habitats (Orloff 1988). They occur up to 2800 m in elevation (Gehrt

2003), but are most common below 1400 m and in riparian settings (Poglayen-Neuwall and Toweill 1988), especially near rocky outcroppings. The forest and woodland types with which they associate include pinyon pine, juniper, oak, and upland conifers (Orloff 1988, Alexander et al. 1994). The conservation status of ringtails is poorly understood; they are common enough to be trapped for fur in Arizona, New Mexico, and Texas. But, they are fully protected in California, and were thought to be declining in Colorado from 1967 to 1973 (Willey and Richards 1974).

Kinds of resting sites and dens used by ringtails are similar to those for raccoons: rock crevices, cavities in trees or snags, and ground burrows dug by other mammals. Ringtails in Oregon tended to den in Douglas-fir snags 15–30 m tall, but occupied areas that were mostly regenerating (5- to 30-year-old) Douglas-fir (Alexander et al. 1994). So, forestry practices that retain large trees, but include early seres, may be beneficial to this species. Being smaller than raccoons, ringtails should have more potential predators, and physical structure could be correspondingly more important. Diets of ringtails are diverse as for other northern procyonids, but include few aquatic foods and tend to favor small vertebrates: rodents, lizards, and birds. Other foods include insects, fruit, and carrion (Gehrt in press). Lacking more specific information about the habitat needs of this species, it is difficult to identify management approaches that will favor or mitigate impacts on them.

Semi-aquatic species

Mink

The American mink lives in wetlands, along watercourses and lakes, and on coastlines. The permanence of water, proximity to water (Allen 1984) and water quality (Osowski et al. 1995) have been shown to be important predictors of habitat value to minks. Vegetation types with which minks associate are highly varied, ranging from emergent herbs in marshes to stream banks, lakeshores, riparian shrub thickets, and riparian forests. In coastal settings, minks forage primarily in the intertidal zone (Hatler 1976), and short intertidal lengths are preferred (Johnson 1985), as for river otters. Selection for specific timber types is difficult to isolate from other habitat factors, however woody structures, particularly CWD, have appeared important for resting in Idaho (Melquist et al. 1981). Especially in Europe, where the American mink has been studied intensively, resting and denning structures associated with trees have been found to be important (Birks and Linn 1982). In marshes, minks commonly rest and

den in abandoned muskrat burrows. Johnson (1985) noted that minks in southeast Alaska were more common than expected on beach segments bordered by clear-cuts, compared to uncut old-growth forest. Clearly, the knowledge base for mink ecology is not sufficient for specific habitat prescriptions for upland coniferous forests. However, the importance of physical structure, including woody vegetation and CWD in riverine settings, seems generally clear.

River otter

River otters occur in marine and freshwater habitats over much of the West. Distribution apparently responds to water quality, and densities tend to be highest in unpolluted coastal waters protected from strong wave action, estuaries, lower stretches of rivers, and coastal marshes (Melquist and Dronkert 1987). After a period of widespread scarcity across the West, natural colonization of otters out of refugia such as Yellowstone National Park has restored parts of the former range (Buskirk 1999). Similarly, widespread re-introductions, not well mapped, have restored parts of the original distribution, including that in southern Colorado and northern Utah.

Diets vary geographically, but are dominated by aquatic prey, particularly fish commonly described as "coarse" or slow-swimming (e.g. sculpins (Cottidae), whitefish (Salmonidae)) and crustaceans. Broad habitat types preferred by river otters vary with season, partly as a function of ice conditions (Reid et al. 1994), which can dramatically affect movements between water and resting sites. Otters in central Idaho preferred valley bottoms to fast-flowing mountain streams, although otters used the latter to access ponds and reservoirs (Melquist and Hornocker 1983). Similarly, otters in arid northeastern Nevada preferred low-gradient streams to high-gradient streams (Bradley 1986). Two factors important to river otters are of particular interest relative to the management of coniferous forests. The first is the overriding importance of woody vegetation, directly and indirectly, to otters, particularly in the interior West. Otters are associated with shrubs and trees directly via log jams and other woody structure used for resting, and indirectly by associating closely with beavers, which require woody vegetation for food, lodges, and dams (Bradley 1986). Otters in Idaho used bank dens and stick lodges of beavers and log jams for resting (Melquist and Hornocker 1983), and those in Nevada were positively associated with the abundance of beavers (Bradley 1986). The second important factor is the proximity of the physical

structure where they can rest to water where they can forage. Larsen (1983) found in southeast Alaska that river otters foraging in marine waters preferred to rest in forest <20 m from the shoreline, with a short intertidal length. Melquist and Hornocker (1983) showed that otters in Idaho avoided even high-quality foraging waters if using them required crossing broad open beaches or mudflats to reach resting sites. The proximity of human activities did not prevent habitat use by otters, unless the otters were harassed.

Otters are fully protected over most of the southern part of their western range, but are trapped for fur in the North, and are taken incidentally to beavers wherever the latter are trapped. Forestry management practices that protect streamside woody vegetation, that do not reduce beaver densities, and that retain woody structures near the edges of permanent water should mitigate the effects of timber harvesting on river otters.

Life needs met by forested habitats

Understanding how forests meet specific life needs of animals helps to predict how forest management will affect those animals. For example, knowing that a species avoids predation on its young by giving birth in bole cavities will suggest that reducing the availability of bole cavities may increase neonatal losses to predators. However, it may not; the habitat feature in most cases will not have been shown specifically to limit the distribution or abundance of the species of interest. Often an alternate, unstudied habitat feature can be substituted for one that is removed, with no perceptible loss to the population. This approach – observing some pattern of resource selection and assuming that the resource is limiting – is common, and is one of the few approaches available to resource managers in the face of biological uncertainty (Ruggiero and McKelvey 2000). Among the needs of small and mid-sized carnivores likely to be addressed by forested habitats, the following seem particularly important.

The need for predator escape and avoidance

Most, if not all, small and mid-sized carnivores are vulnerable to predation and aggression by larger-bodied carnivores (Buskirk 1999). One of the most common ways these species avoid predation is by sheltering themselves with a physical structure, which can take the form of burrows, rock crevices, bole cavities, tree branches, log jams, shrubs, and CWD on the forest floor. Of these, some (e.g., burrows, rock crevices) are found

in non-forested habitats, but forests are unique among major biomes in the amount of above-ground physical structure they provide. Gray foxes, martens, fishers, river otters, raccoons, ringtails, bobcats, and Canadian lynx are all known to use trees, snags, or CWD to escape predators, and weasels, skunks, and wolverines likely do as well. Martens and fishers are especially averse to traveling in areas without overhead cover (Buskirk and Powell 1994). Rock ledges and outcroppings and boulder fields provide cover for a remarkable range of carnivores, including ringtails, bobcats, and martens. These structures seem to be important mostly for predator avoidance, rather than thermal protection, and are not likely to be affected by forestry practices. Managing for physical structure, especially tree cavities and large-diameter CWD near the ground, is one of the few actions that plausibly could benefit mesocarnivores as a group. Although difficult to generalize, it appears likely that some relationship exists between the size of the animals that need structure and the size of the structures needed. However, species with strong ties to woody structures in some parts of their range can thrive beyond the environmental limits of forests; for example, river otters on the Alaska Peninsula south of the limit of trees.

The need for food

Foods of forest mesocarnivores include a huge range of animals, plants, and fungi: insects, crustaceans, vertebrates from passerine birds to whale carrion, berries, seeds, nuts, and agricultural crops. Although mesocarnivores must respond at some level to site productivity, the tremendous range of foods they eat is produced in such a wide range of environments, and so difficult to measure, that apparent food abundance is not highly predictive of the distribution or abundance of most species. The only possible approach to fulfilling the food needs of mesocarnivores is on a site-specific, species-specific, and time-specific basis, but even this may not be a profitable approach for managers, except via habitat management.

Managing for habitats of the prey of specific mesocarnivores is a common management approach to providing for these species. Red-backed voles (*Clethrionomys* spp.) have well-documented ties to structurally complex mesic coniferous forests, and to large-diameter CWD (Hayes and Cross 1987). Snowshoe hares, by contrast, are associated with moderate to high densities of small-diameter woody stems within reach of the ground or snow surface, and with overhead cover (Mowat et al. 2000). Pine squirrels (*Tamiasciurus* spp.), northern flying squirrels (*Glaucomys sabrinus*), muskrats (*Ondatra zibethicus*), and grouse (Tetraoninae) also have habitat

needs that have been documented regionally and should be considered in managing for species that eat them.

The need for access to foraging areas

Access to foraging areas relates to some of the same factors as predator avoidance: physical structure and the juxtaposition of foraging areas with resting or denning sites. For river otters and mink, this translates into ice-free routes from foraging areas to resting sites in winter; lakes with complete ice cover become inaccessible, whereas streams with intermittent open leads or passages beneath the ice may facilitate movements from resting to foraging areas. For martens, the proximity of late successional forests to meadow edges is an important factor in winter foraging (Spencer et al. 1983), as is the subnivean structure mentioned previously (Corn and Raphael 1992). Carnivores that are too large for subnivean foraging (e.g., coyotes, bobcats, and red foxes) and that experience high energetic costs of traveling on the snow surface will be more likely to exhibit seasonal migrations to low-elevation areas or south-facing areas with less snow or crusted snow.

The need for protected thermal environments

By nature of their small body sizes, many small carnivores have inherently high mass-specific metabolic rates, along with limited somatic stores that translate into brief fasting endurance times (e.g., Harlow and Buskirk 1991). Such species are likely to enjoy energetic savings by occupying protected microenvironments that can be warmed by convective heat losses. The thermal energetic basis of micro-habitat selection has been shown most clearly for weasels (Casey and Casey 1979) and the marten (Taylor and Buskirk 1994), but likely applies to small-bodied species generally. A wide range of site types could offer energetic savings, but the kinds of resting sites and dens chosen by diverse species from ringtails to river otters suggest that cavities within or partially enclosed by tree boles are especially important.

Habitat features important to mesocarnivores

Many habitat features are potentially important to small and mid-sized carnivores, but only a few of them tend to be studied: those that are most easily measured, yet have strong predictive value.

Vegetative species dominants

Animals select vegetative species dominants for physical, chemical, or other attributes, not for their taxonomic classification. However, the dominance of some plant species dominants so consistently predicts certain environmental conditions that we can generalize about which animal species will occur with which plant species, with low risk of being wrong. Site moisture is a prime example. Jeffrey pine (*Pinus jeffreyi*), and ponderosa pine (*P. ponderosa*) tend to occur on sites with severe summer droughts and historically frequent fires. With exceptions, such sites tend to have sparse regeneration and little structure near the ground, compared with moist-site species such as Engelmann spruce or subalpine fir. Because martens, fishers, and lynx tend to avoid stands with little understory structure, they tend to avoid dry forest types dominated by Jeffrey or ponderosa pine. Another example relates to the production of hard mast; pinyon pines (e.g. *Pinus edulis*) and whitebark pine (*P. albicaulis*), while ecologically very different, both produce fleshy seeds, in great abundance in some years. These nuts can be keystone resources for communities, but where these species produce few or no seeds, mesocarnivores can be expected to be indifferent to them as a food source.

Successional stage

Successional stage is most commonly mentioned as predictive of habitat value for martens, fishers, and bobcats. The first two species tend to be associated with old-growth stands in the temperate West, although martens have been shown to associate with early post-fire seres in the interior North. Bobcats associate with early seres that produce high densities of lagomorphs in the South. Evidence for lynx varies by region, with evidence suggesting the value of early seres on sites with moist growing seasons. This has not been shown for areas with dry summers in the southern part of the range. Wolverines have not been shown to be associated with specific forest successional stages, but the forests they occupy in the temperate West tend to be subalpine, with long fire-return intervals. Thus, the successional stage of coniferous forests is not highly predictive of habitat value for small and mid-sized carnivores in general, and even for single species may have inconsistent or bi-modal effects.

Snow

Snow attributes have potentially strong explanatory power in the distribution and abundance of western carnivores. Indeed, most habitat

attributes dealing with physical structure near the ground must be evaluated in the context of snow depth and characteristics. Thus, CWD close to the ground that provides overhead cover during the snow-off period may, once submerged by snow, serve no function or a different one (e.g., thermal protection). Likewise, snow that impedes movement by all but snow-adapted mammals may, after a brief thaw, develop a crust that allows free movement by many species. Some species, particularly the procyonids, have apparently poor adaptations to snow, and do not occur in the North. Others, like the marten and lynx, are superbly adapted to snow by nature of their light foot loadings, occur only in areas with cold, snowy winters, and likely enjoy competitive advantages over less well-adapted carnivores in extensive areas of soft, deep snow (Buskirk et al. 2000*a*). Snow has been shown to mediate spatial interactions between coyotes and lynx (Murray and Boutin 1991) and between fishers and martens (Krohn et al. 1997), in each case favoring the species with the lightest foot loadings, and presumably greatest ease of travel in deep snow.

Landscape features

Landscape features refer to the amounts and spatial attributes of patch types, including edge densities, road densities, patch connectivity, and amounts of stands in various distance intervals from various structures (e.g., roads and edges). Landscape features are unstudied for most small and mid-sized carnivores. Some evidence suggests that coyotes associate with roads where competition by wolves prevents their use of more remote areas (Thurber et al. 1992), and Buskirk et al. (2000*a*) hypothesized that roads could facilitate movements of coyotes into areas with deep snow in winter. Martens are negatively affected by landscape-scale loss of forest (Bissonette et al. 1997).

Roads

Although recent interest has focused on the effects of roads and vehicles on populations and behaviors of vertebrates (Forman and Alexander 1998), evidence for effects on mid-sized carnivores is scarce and contradictory. A fundamental problem is that the distribution of roads is confounded by other landscape features. For example, roads might be built in productive forests that are chosen for timber harvest, so that isolating the effect of roads from the productivity of the site can be difficult (Cooperrider et al. 1999). Likewise, roads exert influences through various means, including reducing forest cover, improving access for trappers (Hodgman et al.

1994), increasing sedimentation into streams, and providing access for competing carnivores, so that proximal effects may be difficult to isolate. Wolves are important community structuring agents among carnivores, and the distribution of wolves has been shown in several studies to respond to road densities. Wolves tend to be absent where road densities exceed 0.45 km/km^2 (Mladenoff et al. 1995) to 0.6 km/km^2 (Thurber et al. 1994). Bobcats (Lovallo and Anderson 1996, Riley 1999), wolverines (Carroll et al. 2001), lynx (Apps 2000), and martens (Robitaille and Aubry 2000) have been shown to prefer habitats with low densities of roads, avoid crossing roads within their home ranges, or avoid roads in proportion to traffic levels. Lynx in northern Washington, by contrast, were found to use habitats without apparent influence from roads (McKelvey et al. 2000*b*), and habitats selected by lynx and fishers in the northern Rockies did not respond to road densities (Carroll et al. 2001). Where analyzed, more developed roads (paved, with higher vehicle speeds) tend to have stronger behavioral effects on carnivores.

Non-habitat features

Inter-specific competition

Small and mid-sized carnivores are strongly affected by inter-specific competition and intraguild predation, which are difficult to distinguish from each other in the field. A wide range of species is implicated in these interactions, which are known from various kinds of data: inverse population fluctuations (Latham 1952), aggression directly observed or inferred at necropsy (Schamel and Tracy 1986), and lack of sympatry attributed to competitive exclusion (Krohn et al. 1995). The species involved in these interactions are remarkably diverse and include virtually all those treated here. Coyotes are commonly dominant over smaller canids, bobcats, and lynx (reviewed by Buskirk 1999) and lynx are notorious enemies of red foxes (Stephenson et al. 1991). Fishers are competitively dominant over American martens in settings where snow is shallow or crusted (Krohn et al. 1997). Almost invariably, larger-bodied species dominate interactions with smaller ones, and interactions tend to be stronger between species of similar body form and niche (e.g., coyote and foxes) than between species with highly dissimilar shapes (e.g., otters and badgers). Relative body size also is an important predictor of these interactions. For example, brown bears (*Ursus arctos*, ca. 10^2 kg body weight) compete little with weasels (ca. 10^{-2} kg), but compete fiercely with slightly smaller black

bears (*U. americanus*) (Mattson et al. 1992). These interactions are increasingly recognized as fundamental to community structure of carnivores, and are invoked to explain the absence of some species from some sites (e.g., Crooks and Soulé 1999).

Environmental contaminants

Although a number of causes of acute intoxication of wildlife have been reported, chronic exposure to environmental contaminants is an increasingly recognized cause of population-level effects on a number of small and mid-sized carnivores. Forest and wildlife managers will need to be cognizant of the range and potential magnitude of these effects, although they will in few cases have access to site-specific monitoring data. Evidence for chronic intoxication in carnivores has been of several kinds. First, pathological lesions in wild carnivores consistent with those expected from a particular contaminant have shown that disease is occurring among wild animals and can be linked to a specific toxin (Wren 1985). A variant of this line of evidence is finding contaminant levels in wild animals greater than those that have been found to cause symptoms, lesions, or death in captive surrogates (Blus and Henny 1990, Osowski et al. 1995). Second, bioaccumulation of contaminants as they ascend food pyramids, or over the life of an individual animal demonstrates the ecological processes expected to affect top carnivores over their lifetimes (Organ 1989). Third, the absence of carnivores from contaminated areas but not in uncontaminated areas would, with replication, tend to support a contaminant-based explanation for such a distributional anomaly (Szumski 1998). All of these lines of evidence have been documented for North American mesocarnivores, particularly of species involved in aquatic food chains. This leads us to hypothesize that chronic exposure to contaminants is a potentially huge, yet poorly understood, problem for mesocarnivores, particularly those that forage in aquatic systems: minks, river otters, and possibly raccoons.

Changing approaches to and priorities for carnivore conservation

Historically, mesocarnivores were appreciated, if at all, primarily for the economic value of their skins. Indeed, a number of species became so valuable that trapping, weakly regulated, led to major population declines. In California, for example, it was clear by the 1920's that the marten, fisher,

and wolverine would require special conservation efforts (Dixon 1924), a concern that recurred in the 1940's (Twining and Hensley 1947). In addition, government agents poisoned and trapped carnivores to protect livestock, and as a general principle of game management. Early conservationists, with little knowledge of the role of carnivores in ecosystems, could predict few tangible consequences of those policies: overabundant ungulates, loss of income from furs, or damage to crops from uncontrolled rodent populations.

The protection of vulnerable fur-bearing species from overexploitation in the mid-1900's was a pivotal conservation measure. This was followed by increased interest in a wide array of species for their intrinsic values and for their contributions to ecosystems. Initially, this increased interest was in individual species at risk, mandated by the Endangered Species Act (ESA). Of the mesocarnivores of western forests, the fisher, wolverine, and lynx have been petitioned for listing under ESA; only the lynx has been listed to date (Federal Register 65(58):16052). A number of other species are protected from trapping, or receive special protection, in individual states or provinces.

The conservation of wild carnivores is shifting away from a focus on individual species and toward the collective role of carnivores in ecosystem functioning (reviewed by Aubry et al. 2003) and monitoring (Noss et al. 1996, Terborgh et al. 1999). Carnivores have two important roles. First, they perform important ecological services, including the cycling of nutrients (Ben-David et al. 1998), transferring energy, completing or interrupting the life cycles of parasites, and structuring the communities of non-prey species, especially each other (Aubry et al. 2003). Several researchers have proposed trophic cascades initiated by carnivores, the effects of which extend to primary producers (McLaren and Peterson 1994, Berger et al. 2001). This "top-down" influence by predators (Matson and Hunter 1992) is supported by anecdotal evidence (predator elimination or introduction: King 1984, McShea et al. 1997; herbivore introduction in the absence of predators, Vitousek 1988) and limited experimental evidence (e.g., Terborgh 1992, Krebs et al. 1995*b*). The extirpation of dominant predators has been described as causing "mesopredator release" (Soulé et al. 1988, Palomares et al. 1995, Crooks and Soulé 1999) wherein the size of the largest predator is reduced by the functional extinction of the previously larger predator, and the newly top predators exert unnaturally high levels of predation on even smaller prey – typically ground-nesting birds and rodents. This form of top-down regulation can feature

the same species playing different roles under different circumstances. For example, where large carnivores are absent, coyotes can serve a top-predator role by suppressing the activities of gray foxes and domestic cats (*Felis domesticus*), which, in turn, benefits small bird and mammal populations (Soulé et al. 1988, Crooks and Soulé 1999). The presence of wolves, however, reduces coyote populations, which is expected to have positive effects on other mesocarnivores and on the prey of coyotes (Buskirk 1999). Not all studies support the "top-down" paradigm (e.g., Ryszkowski et al. 1973, Goszczyński 1977, Erlinge et al. 1984, Jedrzejewska and Jedrzejewski 1998) and some (Wright et al. 1994, Polis and Strong 1996) have argued that top-down control exerted by carnivores in nature is uncommon. Regardless of the strength of individual pathways of influence by carnivores on ecosystems, this recent work highlights the diversity and potentially keystone role of carnivores, including mesocarnivores, in ecosystem function, providing further incentives for their conservation and study.

The second important value of carnivores is that they provide information about the integrity of natural systems. Their large home ranges and low population densities make them vulnerable to declines (Weaver et al. 1996, Minta et al. 1999) and, therefore, sensitive indicators of environmental change (Clark et al. 1996, Noss et al. 1996). Species considered here that appear to have the greatest potential as indicators are: (1) those that specialize on late-successional forests (e.g., marten, fisher); (2) those that forage in aquatic environments where contaminants tend to concentrate (e.g., river otter, mink); and (3) those whose space needs are extremely large (e.g., wolverine, lynx).

Considering these important roles of mesocarnivores in natural communities, it is unfortunate that our knowledge of their distributions and abundances in the West is so poor. The declining role of fur-trapping in society means a loss of distributional and demographic information that was generated by fur harvests at little public cost. A number of nonlethal approaches to surveying carnivores (e.g., Zielinski and Kucera 1995) have substituted for this information. Methods that record the tracks of a species on a prepared surface (Zielinski 1995), or that photograph animals remotely (Kucera et al. 1995) have been used to map the distributions of some mesocarnivores (e.g. Kucera et al. 1995, Zielinski et al. 1995) and have been proposed as a means to monitor changes in populations (Zielinski and Stauffer 1996). Similar data have been used to produce regional habitat models (Carroll et al. 1999*b*), which could not have been imagined before remotely sensed satellite images of vegetation,

topography, and climate. Output from these models can be used to compare the habitat suitability of lands with different management histories (Carroll et al. 1999*b*). In addition, habitat models developed for separate species can be compared to understand the habitat attributes that are of common value, versus the attributes that separate the needs of species from each other (e.g., Lindenmayer and Lacy 1995, Carroll et al. 1999*b*, 2001). Even the compilation of carnivore sightings, if screened for reliability, can provide important information about distribution (e.g., Aubry and Houston 1992) and can be used to model and predict habitat use (Palma et al. 1999, Carroll et al. 2001). The remote collection of genetic samples from either hairs or scats (Foran et al. 1997) will likewise provide understanding of mesocarnivore populations.

These detection methods make it possible to address the distribution and abundance of mesocarnivores at various spatial scales. Traditionally, the study of habitat has focused on stand-level attributes, or the aggregation of stand information for analysis at the level of the home range. The consideration of regional-scale influences on carnivore populations is relatively new, but such analyses can suggest habitat factors not evident from smaller-scale field studies. For example, correlations between fisher occurrences and such regional factors as elevation, distance to the ocean, precipitation, and other geographical variables (Klug 1996, Carroll 1997) may be as strong as, or stronger than, within-patch, home range, or even landscape-level habitat variables (Carroll et al. 1999*a*). The relative contribution of different scales of habitat influence on distribution or abundance has rarely been evaluated for mesocarnivore species, but is profoundly important to managers.

Determining the current distribution of mesocarnivores is the first step toward understanding their status and the first priority for their conservation. Surveys can collect information simultaneously on most species of mammals that are attracted to meat baits. Systematic surveys are also an ideal means to locate patchily distributed populations, even those that have gone undetected for decades using other methods (e.g., the Humboldt marten (*Martes americana humboldtensis*) (Zielinski et al. 2001)). Such large-scale surveys complement, and in some cases substitute for, data acquired via traditional telemetry studies. The latter method usually is limited to a relatively small area of a species' range and usually where the species is common, limiting inferences about areas where it is rare. We suggest that periodic extensive surveys are the best foundation for conserving mesocarnivores in western forests. They can describe current

geographical range, be used to develop habitat models at scales that are relevant for decision-making, and provide information on abundance.

The concept of a metapopulation (Levins 1968, Wright 1978, Harrison and Taylor 1997) linked by occasional dispersal may be especially applicable to the conservation of mature-forest specialists in the fragmented habitats of western North America. Unlike birds, forest mammals, particularly the late-successional specialists, are fairly dispersal-sensitive, strongly preferring to travel under dense tree canopies (Buskirk and Powell 1994). The discontinuous patterns of habitat for fishers in the West (Weir and Harestad 1997, Carroll et al. 1999*a*) and for martens on mountain-top islands (Wisz 1999) are examples of habitat discontinuities that could give rise to metapopulations. Alternatively, these spatially structured populations could have the properties of source-sink systems (Pulliam 1996), in which the gradients of dispersal are consistently away from areas that produce a surplus of animals and toward areas that require dispersive inputs for their populations to persist. If clusters of suitable habitat for a species become too small or isolated, the imbalance between immigration and emigration can affect viability (Noon and McKelvey 1996). The decline in distribution of fishers (Powell and Zielinski 1994) and wolverines (Banci 1994) may be due to such regional-level dynamics. Dispersal limitation may affect regional population viability by reducing the connections between subpopulations and lowering the likelihood that suitable habitat patches are colonized and re-colonized over time (Fahrig and Paloheimo 1988). The conservation of forest habitat specialists, such as the fisher, lynx, and marten, as well as other species that require wilderness conditions (e.g., wolverine) will require planning to protect large blocks of suitable habitat and the connections between them (Bissonette and Broekhuizen 1995).

Mesocarnivores in conservation planning

Managing ecosystems requires monitoring the composition, structure, and function of the system. The large area requirements, top trophic status, and low population densities shared by many carnivore species make them ideally suited as indicators of ecosystem integrity and, therefore, as tools for addressing the conservation of ecosystems (Noss et al. 1996, Terborgh et al. 1999). Whether carnivores serve as keystone species in forest ecosystems or not (Mills et al. 1993, Noss et al. 1996), their relatively large area requirements suggest that, if their populations are abundant

and well-distributed, the habitat – and perhaps the populations – of many other species will also be protected (Noss and Cooperrider 1996:162). The area requirements and dispersal limitation of some mesocarnivores qualify them as "focal species" for conservation planning (Noss et al. 1996, Lambeck 1997, Carroll et al. 2001).

The utility of carnivores in large-scale conservation planning is exemplified by The Wildlands Project (Foreman et al. 1992, Noss 1992) which has codified its approach to ecosystem protection and planning under the guidance of the "3 Cs": carnivores, cores and connectivity. The size of core areas is determined by the area needed by a subpopulation of focal carnivore species. Protected core areas are the central elements of conservation planning and are similar to the concept of refugia, which have previously been promoted as a means of conserving forest carnivores (de Vos 1951, Buskirk 1994). These core areas are then connected via corridors that are selected to facilitate the movement of the focal carnivores, and other ecosystem components and processes, between core areas. By considering the needs of carnivores, the planner has an objective basis for determining the optimal size of reserve networks (Noss et al. 1996).

Most often it is the large carnivores (wolves, grizzly bears, mountain lions (*Felis concolor*)) that are considered the most useful species for conservation planning. This is primarily due to their large spatial needs, but is probably also influenced by their charismatic appeal to the public. Conservation biologists have recognized that mesocarnivores can have the same role, not only because the home range sizes of some species (i.e., wolverine, lynx) are similar to or greater than those of large carnivores, but because the extirpation of large carnivores in many regions has promoted mesocarnivores to the role of top predators. Including a combination of focal carnivore species, especially mesocarnivores that specialize on habitats of concern, may ultimately be the best approach to large-scale conservation. This is because large carnivores are often generalists whose habitats may not include environments with high value for biodiversity (Noss et al. 1996). Carroll et al. (2001) developed regional habitat models for wolverine, lynx, grizzly bear, and fisher in the Rocky Mountains and found that the occurrence of wolverines and grizzly bears was strongly associated with low levels of roads and human population density, whereas fishers and lynx were less influenced by the density of humans but more affected by the density and extent of low-elevation, productive forests. These results, and those of a similar study that included ten species of carnivores (Carroll et al. 2001), indicate that a comprehensive conservation strategy for carnivores in the

Rocky Mountains should consider the needs of several carnivore species rather than a single presumed umbrella species.

Recent policy developments in the management of federal lands in the United States suggest that regional-scale dynamics are appreciated and considered in land-management planning (e.g., Interior Columbia River Basin Ecosystem Management Project USDA 1996, Northwest Forest Plan, USDA and USDI 1994, Sierra Nevada Framework, USDA 2001). However, many planning processes are still poorly adapted to decision-making across jurisdictional boundaries. Information at the regional scale is the dominant source of knowledge for long-term and large-scale conservation planning (Clark and Minta 1994, Mladenoff et al. 1995, Soulé and Terborgh 1999). If we are to maintain viable populations of species that have large home ranges and are vulnerable to human activities, then the "conservation planner must grabble with the design and management of entire landscapes" (Noss et al. 1996). The conservation of carnivores in landscapes is as much a policy issue as a scientific one (Clark et al. 1996, Primm and Clark 1996). Biological science is fundamental to strategies for conserving mesocarnivores, but political solutions will require integration with the social sciences, education, and law. Therein lies an imposing challenge for coming decades.

Summary

Small and mid-sized carnivores of western forests represent an ecologically diverse and influential guild of forest vertebrates. They comprise over a dozen species with varied life histories and habitat associations, highly species-specific responses to human-caused habitat change, and varied conservation status across western North America. Forested habitats fulfill various of their life needs, including the need for predator escape and avoidance (e.g., marten and river otter), for protected thermal environments (e.g., marten), for specialized foods (e.g., lynx) and for access to specialized foraging areas (e.g., ermines). For several species, the specific life needs fulfilled by forested habitats can only be inferred. Vegetative species dominants are somewhat predictive of the distribution and abundance of mesocarnivores, inasmuch as moist-site species tend to be associated with long fire-return intervals, and seed-producing species (e.g., whitebark pine) attract certain species. Successional stage is highly predictive of the distribution and abundance of some species, particularly martens, fishers, and bobcats, but not at all for others. Several

species (e.g., coyote, river otter, ermine) are facultative forest associates and widely distributed and abundant far from trees. The effects of landscape pattern on the distribution and abundance of mid-sized carnivores are just beginning to be understood, with percent of an area in uncut forest, road density, and edge density having been shown important predictors. Inter-specific competition is a powerful influence on the distribution and abundance of mesocarnivores, with size-mediated (top-down) effects known for most species treated here. By the nature of their high trophic positions, carnivores, particularly those that participate in aquatic food webs, are vulnerable to individual- and population-level contaminants, including those introduced or mobilized by human actions. Our values regarding and approaches to monitoring mid-sized carnivores have shifted from managing them for fur and to minimize their depredations to valuing them more broadly. Today, the values attached to them are more intrinsic and esthetic, and related to their contributions to community and ecosystem processes. They are also important tools for monitoring the status of natural systems at various spatial and ecological scales. Large carnivores are more commonly used in conservation plannning, but the habitat specialization and huge spatial requirements of some mesocarnivores may make them more suitable and more constraining conservation planning tools.

Literature cited

Alexander, L.F., B.J. Verts, and T.P. Farrell. 1994. Diet of ringtails (*Bassariscus astutus*) in Oregon. *Northwestern Naturalist* 75:97–101.

Allen, A.W. 1984. Habitat suitability index models: mink. US Fish and Wildlife Service **FWS/OBS-82/10.61** Revised. 19pp.

Apps, C.D. 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains: a study. Pages 351–371 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

Aubry, K.B. 1983. The Cascade red fox: distribution, taxonomy, zoogeography and ecology. Dissertation. University of Washington, Seattle, Washington, USA.

Aubry, K.B. 1984. The recent history and present distribution of the red fox in Washington. *Northwest Science* **58**:69–79.

Aubry, K.B. and D.B. Houston. 1992. Distribution and status of the fisher (*Martes pennanti*) in Washington. *Northwestern Naturalist* 73:69–79.

Aubry, K.B., F.E. Wahl, J. Von Kienast, T.J. Catton, and S.G. Armentrout. 1997. Use role of remote video cameras for the detection of forest carnivores and in radio-telemetry studies of fishers. Pages 350–361 *in* G. Proulx, H.N. Bryant, and

P.M. Woodard, editors. Martes: *Taxonomy, Ecology, Techniques, and Management*. Provincial Museum of Alberta, Edmonton, Alberta, Canada.

Aubry, K.B., G.M. Koehler, and J.R. Squires. 2000. Ecology of Canada lynx in southern boreal forests. Pages 373–396 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

Aubry, K.B., J.P. Hayes, B.L. Biswell, and B.G. Marcot. 2003. The ecological role of tree-dwelling mammals in western coniferous forests. Pages 405–443 *in* C.J. Zabel and R.G. Anthony, editors. *Mammal Community Dynamics. Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, Cambridge, UK.

Bailey, V. 1936. The mammals and life zones of Oregon. *North American Fauna* **55**: 1–416.

Baker, J.M. 1992. Habitat use and spatial organization of pine marten on southern Vancouver Island, British Columbia. M.S. Thesis. Simon Fraser University, Burnaby, British Columbia, Canada.

Banci, V.A. 1987. Ecology and behavior of wolverine in Yukon. M.S. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Banci, V.A. 1994. Wolverine. Pages 99–127 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, editors. The scientific basis for conserving forest carnivores, American marten, fisher, lynx, and wolverine in the western United States. USDA Forest Service General Technical Report **RM-254**, Fort Collins, Colorado, USA.

Ben-David, M., T.A. Hanley, and D.M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* **83**:47–55.

Berger, J., P.B. Stacey, L. Bellis, and M.P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications* **11**:947–960.

Birks, J.D.S. and I.J. Linn. 1982. Studies of home range of the feral mink (*Mustela vison*). *Symposia of the Zoological Society of London* **49**:231–257.

Bissonette, J.A. and S. Broekhuizen. 1995. Martes populations as indicators of habitat spatial patterns: the need for a multiscale approach. Pages 95–121 *in* W.Z. Lidicker, Jr., editor. *Landscape Approaches in Mammalian Ecology and Conservation*. University of Minnesota Press, Minneapolis, Minnesota, USA.

Bissonette, J.A., D.J. Harrison, C.D. Hargis, and T.G. Chapin. 1997. The influence of spatial scale and scale-sensitive properties on habitat selection by American marten. Pages 368–385 *in* J. A. Bissonette, editor. *Wildlife and Landscape Ecology*. Springer-Verlag, New York, NY, USA.

Blus, L.J. and C.J. Henny. 1990. Lead and cadmium concentrations in mink from northern Idaho. *Northwest Science* **64**:219–223.

Bradley, P.V. 1986. Ecology of river otters in Nevada. M.S. Thesis, University of Nevada, Reno, NV, USA.

Buck, S., C. Mullis, and A. Mossman. 1994. Habitat use by fishers in adjoining heavily and lightly harvested forest. Pages 368–376 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, USA.

Buskirk, S.W. 1984. Seasonal use of resting sites by marten in southcentral Alaska. *Journal of Wildlife Management* **48**:950–953.

Buskirk, S.W. 1994. The refugium concept and the conservation of forest carnivores. Pages 242–245 *in Proceedings of the XXI International Congress of Game Biologists*, Halifax, Nova Scotia, Canada.

Buskirk, S.W. 1999. Mesocarnivores of Yellowstone. Pages 165–187 *in* T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva, editors. *Carnivores in Ecosystems: the Yellowstone Experience.* Yale University Press, New Haven, Connecticut, USA.

Buskirk, S.W. and S.O. MacDonald. 1984. Seasonal food habits of marten in south-central Alaska. *Canadian Journal of Zoology* **62**:944–950.

Buskirk, S.W. and R.A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283–296 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation.* Cornell University Press, Ithaca, New York, USA.

Buskirk, S.W. and L.F. Ruggiero. 1994. American marten. Pages 38–73 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, editors. The scientific basis for conserving forest carnivores, American marten, fisher, lynx, and wolverine in the western United Statees. U.S. Forest Service General Technical Report **RM-254**, Fort Collins, Colorado, USA.

Buskirk, S.W., L.F. Ruggiero, and C.J. Krebs. 2000*a*. Habitat fragmentation and interspecific competition: implications for lynx conservation. Pages 83–100 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States.* University Press of Colorado, Boulder, Colorado, USA.

Buskirk, S.W., L.F. Ruggiero, K.B. Aubry, D.E. Pearson, J.R. Squires, and K.S. McKelvey. 2000*b*. Comparative ecology of lynx in North America. Pages 397–417 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States.* University Press of Colorado, Boulder, Colorado, USA.

Carey, A.B. and J.E. Kershner. 1997. *Spilogale gracilis* in upland forests of western Washington and Oregon. *Northwestern Naturalist* 77:29–34.

Carroll, C. 1997. Predicting the distribution of the fisher (*Martes pennanti*) in northwestern California, USA, using survey data and GIS modeling. M.S. Thesis. Oregon State University, Corvallis, Oregon, USA.

Carroll, C., W.J. Zielinski, and R.F. Noss. 1999*a*. Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath Region, U.S.A. *Conservation Biology* 13:1344–1359.

Carroll, C., P.C. Paquet, and R.F. Noss. 1999*b*. *Modeling Carnivore Habitat in the Rocky Mountain Region: a Literature Review and Suggested Strategy*. World Wildlife Fund, Toronto, Ontario, Canada.

Carroll, C., R.F. Noss, and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* 11:961–980.

Casey, T.M. and K.K. Casey. 1979. Thermoregulation of arctic weasels. *Physiological Zoology* **52**:153–164.

Chamberlain, M.J., K.M. Hodges, B.D. Leopold, and T.S. Wilson. 1999. Survival and cause-specific mortality of adult raccoons in central Mississippi. *Journal of Wildlife Management* **63**:880–888.

Chapin, T.G., D.J. Harrison, and D.D. Katnik. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. *Conservation Biology* **12**:1327–1337.

Clark, T.W. and S.C. Minta. 1994. *Greater Yellowstone's Future: Prospects for Ecosystem Science, Management, and Policy*. Homestead Press, Moose, Wyoming, USA.

Clark, T.W., A.P. Curlee, and R.P. Reading. 1996. Crafting effective solutions to the large carnivore conservation problem. *Conservation Biology* **10**:940–948.

Cooperrider, A., R.F. Noss, H.H. Welsh, Jr., C. Carroll, W. Zielinski, D. Olson, S.K. Nelson, and B.G. Marcot. 1999. Terrestrial fauna of redwood forests. Pages 119–163 *in* R.F. Noss, editor. *The Redwood Forest*. Island Press, Washington DC, USA.

Copeland, J.P. 1996. Biology of the wolverine in central Idaho. M.S. Thesis. University of Idaho, Moscow, Idaho, USA.

Corn, J.G. and M.G. Raphael. 1992. Habitat characteristics at marten subnivean access sites. *Journal of Wildlife Management* **56**:442–448.

Crabb, W.D. 1941. Food habits of the prairie spotted skunk in southeastern Iowa. *Journal of Mammalogy* **22**:349–364.

Crabb, W.D. 1948. The ecology and management of the prairie spotted skunk in Iowa. *Ecological Monographs* **18**:201–232.

Crabtree, R. 1993. Gray ghost of the Beartooth. *Yellowstone Science* **1**(spring):13–16.

Crooks, K.R. and M.E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**:563–566.

Crooks, K.R. and D. Van Vuren. 1995. Resource utilization by 2 insular endemic mammalian carnivores, the island fox and island spotted skunk. *Oecologia* **104**:301–307

de Vos, A. 1951. Ecology and management of fisher and marten in Ontario. Ontario Department of Lands and Forests, Technical Bulletin, Wildlife Service **1**: 1–90.

Dixon, J. 1924. A closed season needed for fisher, marten and wolverine in California. *California Department of Fish and Game* **11**:23–25.

Dorney, R.S. 1954. Ecology of marsh raccoons. *Journal of Wildlife Management* **18**: 217–225.

Dragoo, J.W. and R.L. Honeycutt. 1997. Systematics of mustelid-like carnivores. *Journal of Mammalogy* **78**:426–443.

Edelmann, F. and J. Copeland. 1999. Wolverine distribution in the northwestern United States and a survey in the Seven Devils Mountains of Idaho. *Northwest Science* **73**:295–300.

Erlinge, S., G. Goransson, G. Hogstedt, G. Jansson, O. Liberg, J. Loman, I.N. Nilsson, T. Von Schantz, and M. Sylven. 1984. Can vertebrate predators regulate their prey? *American Naturalist* **123**:125–133.

Fagerstone, K.A. 1987. Black-footed ferret, long-tailed weasel, short-tailed weasel, and least weasel. Pages 549–573 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Fahrig, L. and J. Paloheimo. 1988. Effect of spatial arrangement of habitat patches on local population size. *Ecology* **69**:468–475.

Fitzgerald, B.M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *Journal of Animal Ecology* **46**:367–397.

Foran, D.R., S.C. Minta, and K.S. Heinemeyer. 1997. DNA-based analysis of hair to identify species, gender, and individuals for population research and monitoring. *Wildlife Society Bulletin* **25**:840–847.

Foreman, D., J. Davis, D. Johns, R. Noss, and M.E. Soule. 1992. The Wildlands Project mission statement. *Wild Earth* (special issue) **2**–3.

Forman, R.T.T. and L.E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**:207–231.

Fuller, A.K. 1999. Influence of selection harvesting on American marten and their primary prey in northcentral Maine. M.S. Thesis. University of Maine, Orono, Maine, USA.

Fuller, T.K. 1978. Variable home-range sizes of female gray foxes. *Journal of Mammalogy* **59**:446–449.

Fuller, T.K., W.E. Berg, and D.W. Kuehn. 1985. Survival rates and mortality factors of adult bobcats in north-central Minnesota. *Journal of Wildlife Management* **49**:292–296.

Gardner, C.L. 1985. The ecology of wolverines in southcentral Alaska. M.S. Thesis. University of Alaska, Fairbanks, Alaska, USA.

Gehrt, S.D. 2003. Raccoon and allies. *In* G. Feldhamer, B. Thompson, and J. Chapman, editors. *Wild Mammals of North America*. Second Edition. Johns Hopkins University Press, Baltimore, Maryland, USA: in press.

Gibilisco, C.J. 1994. Distributional dynamics of modern *Martes* in North America. Pages 59–71 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, USA.

Gilbert, F.F. and R. Allwine. 1991. Small mammal communities in the Oregon Cascade Range. Pages 269–284 *in* Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report **PNW-285**, Portland, Oregon, USA.

Godin, A.J. 1982. Striped and hooded skunks. Pages 674–687 *in* J.A. Chapman and G.A. Feldhamer, editors. *Wild Mammals of North America*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Goszczyński, J. 1977. Connections between predatory birds and mammals and their prey. *Acta Theriologica* **22**:399–430.

Grenfell, W.E. and M. Fasenfest. 1979. Winter food habits of fishers, *Martes pennanti*, in northwestern California. *California Fish and Game* **65**:186–189.

Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1937. *Fur-bearing Mammals of California: their Natural History, Systematic Status, and Relations to Man*. Volumes 1, 2. University of California Press, Berkeley, California, USA.

Hagmeier, E.M. 1956. Distribution of marten and fisher in North America. *Canadian Field-Naturalist* **70**:149–168.

Hamilton, W.J., Jr. 1933. The weasels of New York. *American Midland Naturalist* **14**:289–344.

Hargis, C.D., J.A. Bissonette, and D.L. Turner. 1999. Influence of forest fragmentation and landscape pattern on American martens. *Journal of Applied Ecology* **36**:157–172.

Harlow, H.J. and S.W. Buskirk. 1991. Comparative serum and urine chemistry of fasting white-tailed prairie dogs (*Cynomys leucurus*) and American martens (*Martes americana*): representative fat and lean-bodied animals. *Physiological Zoology* **64**:1261–1278.

Harrison, R.L. 1997. A comparison of gray fox ecology between residential and undeveloped rural landscapes. *Journal of Wildlife Management* **61**:112–122.

Harrison, S. and A.D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 *in* I. Hanski and M. E. Gilpin, editors. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA.

Hartman, L.H. and D.S. Eastman. 1999. Distribution of introduced raccoons *Procyon lotor* on the Queen Charlotte Islands: implications for burrow-nesting seabirds. *Biological Conservation* **88**:1–13.

Hash, H.S. 1987. Wolverine. Pages 575–585 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resources, Ontario, Canada.

Hatler, D.F. 1976. The coastal mink on Vancouver Island, British Columbia. PhD Thesis, University of British Columbia, Vancouver, British Columbia, Canada.

Hawley, V.D. and F.E. Newby. 1957. Marten home ranges and population fluctuations in Montana. *Journal of Mammalogy* **38**:174–184.

Hayes, J.P. and S.P. Cross. 1987. Characterization of logs used by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. *Canadian Field-Naturalist* **101**:543–546.

Heinemeyer, K.S. 1993. Temporal dynamics in the movements, habitat use, activity, and spacing of reintroduced fishers in northwestern Montana. M.S. Thesis. University of Montana, Missoula, Montana, USA.

Henke, S.E. and F.C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management* **63**:1066–1081.

Hodges, K.E. 2000. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

Hodgman, T.P., D.J. Harrison, D.D. Katnik, and K.D. Elowe. 1994. Survival in an intensively trapped marten population in Maine. *Journal of Wildlife Management*. **58**:593–600.

Hooven, E.F. and H.C. Black. 1976. Effects of some clear-cutting practices on small-mammal populations in western Oregon. *Northwest Science* **50**:189–208.

Hornocker, M.G. and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology* **59**:1286–1301.

Jedrzejewska, B. and W. Jedrzejewski. 1998. *Predation in Vertebrate Communities: the Białowieża Primeval Forest as a Case Study*. *Ecological Studies*. Volume 135, Springer-Verlag, New York, New York, USA.

Johnson, C.B. 1985. Use of coastal habitat by mink on Prince of Wales Island, Alaska. M.S. Thesis, University of Alaska, Fairbanks, Alaska, USA.

Jones, J.L. and E.O. Garton. 1994. Selection of successional stages by fishers in northcentral Idaho. Pages 377–388 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, USA.

Kelly, G.M. 1977. Fisher (*Martes pennanti*) biology in the White Mountain National Forest and adjacent areas. Dissertation. University of Massachusetts, Amherst, MA, USA.

King, C. 1984. *Immigrant Killers: Introduced Predators and the Conservation of Birds in New Zealand*. Oxford University Press, New York, New York, USA.

Klug, R.R. 1996. Occurrence of Pacific fisher in the redwood zone of northern California and the habitat attributes associated with their detection. M.S. Thesis. Humboldt State University, Arcata, California, USA.

Koehler, G.M. and M.G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. *Journal of Mammalogy* 72:391–396.

Krebs, C.J., S. Boutin, R. Boonstra, A.R.E. Sinclair, J.N.M. Smith, M.R.T. Dale, and M.R. Turkington. 1995*b*. Impact of food and predation on the snowshoe hare cycle. *Science* **269**:1112–1115.

Krebs, J.W., M.L. Wilson, and J.E. Childs. 1995*a*. Rabies – epidemiology, prevention and future research. *Journal of Mammalogy* 76:681–694.

Krohn, W.B., K.D. Elowe, and R.B. Boone. 1995. Relations between fishers, snow, and martens: development and evaluation of two hypotheses. *Forestry Chronicle* 71:97–105.

Krohn, W.B., W.J. Zielinski, and R.B. Boone. 1997. Relations among fishers, snow, and martens in California: results from small-scale spatial comparisons. Pages 211–232 *in* G. Proulx, H.N. Bryant, and P.M. Woodard, editors. Martes: *Taxonomy, Ecology, Techniques, and Management*. Provincial Museum of Alberta, Edmonton, Alberta, Canada.

Kucera, T.E., W.J. Zielinski, and R.M. Barrett. 1995. The current distribution of American marten, *Martes americana,* in California. *California Fish and Game* **81**:96–103.

Lambeck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* **11**:849–856.

Larsen, D.N. 1983. Habitats, movements, and foods of river otters in coastal southeastern Alaska. M.S. Thesis, University of Alaska, Fairbanks, Alaska, USA.

Latham, R.M. 1952. The fox as a factor in the control of weasel populations. *Journal of Wildlife Management* **16**:516–517.

Levins, R. 1968. *Evolution in Changing Environments*. Princeton University Press, Princeton, New Jersey, USA.

Lewis, J.C. and W.J. Zielinski. 1996. Historical harvest and incidental capture of fishers in California. *Northwest Science* 70:291–297.

Lewis, J.C., R.T. Golightly, and R.M. Jurek. 1995. Introduction of non-native red foxes in California: implications for the Sierra Nevada red fox. *Transactions of the Western Section of the Wildlife Society* 31:29–32.

Lindenmayer, D.B. and R.C. Lacy. 1995. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparisons among species. *Ecological Applications* 5:183–199.

Lovallo, M.J. and E.M. Anderson. 1996. Bobcat movements and home ranges relative to roads in Wisconsin. *Wildlife Society Bulletin* 24:71–76.

Magoun, A.J. and J.P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* **62**:1313–1320.

Maj, M. and E.O. Garton. 1994. Fisher, lynx, wolverine: summary of distribution information. Pages 169–175 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, editors. The scientific basis for conserving forest carnivores, American marten, fisher, lynx, and wolverine in the western United Statees. USDA Forest Service General Technical Report **RM-254**, Fort Collins, Colorado, USA.

Martin, S.K. 1994. Feeding ecology of American martens and fishers. Pages 297–315 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, USA.

Maser, C., B.R. Mate, J. Franklin, and C.T. Dyfress. 1981. Natural history of Oregon Coast mammals. USDA Forest Service General Technical Report **PNW-133**, Portland, Oregon, USA.

Matson, P.A. and M.D. Hunter. 1992. The relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology* 73:723.

Mattson, D.J., R.R. Knight, and B.M. Blanchard. 1992. Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975–1990. *Journal of Mammalogy* 73:422–425.

McCord, C.M. 1974. Selection of winter habitat by bobcats (*Lynx rufus*) on the Quabbin Reservation, Massachusetts. *Journal of Mammalogy* 55:428–437.

McKelvey, K.S., K.B. Aubry, and Y.K. Ortega. 2000*a*. History and distribution of lynx in the contiguous United States. Pages 207–264 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

McKelvey, K.S., Y.K. Ortega, G.M. Koehler, K.B. Aubry, and J.D. Brittell. 2000*b*. Canada lynx habitat and topographic use patterns in north-central Washington: a reanalysis. Pages 307–336 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

McLaren, B.E. and R.O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. *Science* **266**:1555–1558.

McShea, W.J., J.H. Rappole, and H.B. Underwood. 1997. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington DC, USA.

Melquist, W.E. and A.E. Dronkert. 1987. River otter. Pages 627–641 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resources, Ontario, Canada.

Melquist, W.E. and M.G. Hornocker. 1983. Ecology of river otters in west central Idaho. *Wildlife Monographs* 83:1–60.

Melquist, W.E., J.S. Whitman, and M.G. Hornocker. 1981. Resource partitioning and coexistence of sympatric mink and river otter populations. Pages 187–220 *in* J.A. Chapman and D. Pursley, editors. *Worldwide Furbearer Conference Proceedings*, Volume 1. Frostburg, Maryland, USA.

Miller, S.D. 1980. The ecology of the bobcat in south Alabama. Dissertation, Auburn University, Auburn, Alabama, USA.

Mills, L.S., M.E. Soulé, and D.F. Doak. 1993. The keystone species concept in ecology and conservation. *BioScience* 43:219–224.

Minta, S.C., P.M. Kareiva, and A.P. Curlee. 1999. Carnivore research and conservation: learning from history and theory. Pages 323–404 *in* T.W. Clark, S.C. Minta, P.K. Karieva, and A.P. Curlee, editors. *Carnivores in Ecosystems: the Yellowstone Experience*. Yale University Press, New Haven, Connecticut, USA.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* **9**:279–294.

Mowat, G., K.G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pages 265–306 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

Murray, D.L. and S. Boutin. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia* **88**:463–469.

Noon, B.R. and K.S. McKelvey. 1996. Management of the spotted owl: a case history in conservation biology. *Annual Review of Ecology and Systematics* **27**:135–162.

Noss, R.F. 1992. The Wildland Project: land conservation strategy. *Wild Earth* (special issue) **1**:10–25.

Noss, R.F. and A.Y. Cooperrider. 1996. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press, Washington DC, USA.

Noss, R.F., H.B. Quigley, M.G. Hornocker, T. Merrill, and P.C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* **10**:949–963.

O'Donoghue, M., S. Boutin, C.J. Krebs, G. Zuleta, D.L. Murray, and E.J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* **79**:1193–1208.

Organ, J.F. 1989. Mercury and PCB residues in Massachusetts river otters: comparisons on a watershed basis. Dissertation, University of Massachusetts, Amherst, Massachusetts, USA.

Orloff, S. 1988. Present distribution of ringtails in California. *California Fish and Game* **74**:196–202.

Orr, R.T. 1943. Altitudinal record for the spotted skunk in California. *Journal of Mammalogy* **24**:270.

Osowski, S.L., L.W. Brewer, O.E. Baker, and G.P. Cobb. 1995. The decline of mink in Georgia, North Carolina, and South Carolina: the role of contaminants. *Archives of Environmental Contaminants and Toxicology* **29**:418–423.

Palma, L., P. Beja, and M. Rodrigues. 1999. The use of sighting data to analyse Iberian lynx habitat and distribution. *Journal of Applied Ecology* **36**:812–824.

Palomares, F., P. Gaona, P. Ferreras, and M. Delibes. 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Conservation Biology* **9**:294–304.

Paragi, T.F., W.N. Johnson, D.D. Katnik, and A.J. Magoun. 1996. Marten selection of postfire seres in the Alaskan taiga. *Canadian Journal of Zoology* **74**:2226–2237.

Payer, D.C. 1999. Influence of timber harvesting and trapping on habitat selection and demographic characteristics of American marten. Dissertation. University of Maine, Orono, Maine, USA.

Poglayen-Neuwall, I. and D.E. Toweill. 1988. *Bassariscus astutus*. *Mammalian Species* **327**:1–8.

Polis, G.A. and D.R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.

Potvin, F., L. Belanger, and K. Lowell. 2000. Marten habitat selection in a clear-cut boreal landscape. *Conservation Biology* **14**:844–857.

Powell, R.A. 1979. Fishers, population models, and trapping. *Wildlife Society Bulletin* 7:149–154.

Powell, R.A. 1993. *The Fisher: Life History, Ecology and Behavior*. 2nd edition. University of Minnesota Press, Minneapolis, Minnesota, USA.

Powell, R.A. and W.J. Zielinski. 1994. Fisher. Pages 38–73 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, editors. The Scientific Basis for Conserving Forest Carnivores: American marten, fisher, lynx, and wolverine in the western United Statees. USDA Forest Service General Technical Report **RM-254**, Fort Collins, Colorado, USA.

Primm, S.A. and T.W. Clark 1996. Making sense of the policy process for carnivore conservation. *Conservation Biology* **10**:1036–1045.

Pulliam, H.R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45–69 *in* O.E. Rhodes, R.K. Chesser, and M.H. Smith, editors. *Population Biology in Ecological Space and Time*. University of Chicago Press, Chicago, Illinois, USA.

Quick, H.F. 1951. Notes on the ecology of weasels in Gunnison County, Colorado. *Journal of Mammalogy* **32**:281–290.

Ralls, K. and P.J. White. 1995. Predation of San Joaquin kit foxes by larger canids. *Journal of Mammalogy* **76**:723–729.

Reid, D.G., T.E. Code, A.C.H. Reid, and S.M. Herrero. 1994. Spacing, movements, and habitat selection of the river otter in boreal Alberta. *Canadian Journal of Zoology* **72**:1314–1324.

Riley, S.P.D. 1999. Spatial organization, food habits and disease ecology of bobcats (*Lynx rufus*) and gray foxes (*Urocyon cinereoargenteus*) in national park areas in urban and rural Marin County, California. Dissertation, University of California, Davis, California, USA.

Robitaille, J. and K. Aubry. 2000. Occurrence and activity of American martens, *Martes americana*, in relation to roads and other routes. *Acta Theriologica* **45**:137–143.

Rogers, C.M. and M.J. Caro. 1998. Song sparrows, top carnivores, and nest predation: a test of the mesopredator release hypothesis. *Oecologia* **116**:227–233.

Rolley, R.E. 1987. Bobcat. Pages 671–681 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resouces, Ontario, Canada.

Rolley, R.E. and W.D. Warde. 1985. Bobcat habitat use in southeastern Oklahoma. *Journal of Wildife Management* **49**:913–920.

Rosenberg, K.V. and R.G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263–272 *in* J. Verner, M.L. Morrison, C.J. Ralph, editors. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.

Roy, K.D. 1991. Ecology of reintroduced fishers in the Cabinet Mountains of northwest Montana. M.S. Thesis. University of Montana, Missoula, Montana, USA.

Ruggiero, L.F. and K.S. McKelvey. 2000. Toward a defensible lynx conservation strategy: a framework for planning in the face of uncertainty. Pages 5–19 *in* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, editors. 2000. *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.

Ruggiero, L.F., D.E. Pearson, and S.E. Henry. 1998. Characteristics of American marten den sites in Wyoming. *Journal of Wildlife Management* **62**:663–673.

Ryszkowski, L., J. Gozczyński, and J. Truszkowski. 1973. Trophic relationships of the common vole in cultivated fields. *Acta Theriologica* **18**:125–165.

Samuel, D.E. and B.B. Nelson. 1982. Foxes: *Vulpes vulpes* and allies. Pages 475–490 *in* J.A. Chapman, and G.A. Feldhamer, editors. *Wild Mammals of North America: Biology, Management, and Economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Sanderson, G.C. 1987. Raccoon. Pages 487–499 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resources, Ontario, Canada.

Schamel, D. and D.M. Tracy. 1986. Encounters between arctic foxes, *Alopex lagopus*, and red foxes, *Vulpes vulpes*. *Canadian Field-Naturalist* **100**:562–563.

Schempf, P.F. and M. White. 1977. Status of six furbearer populations in the mountains of northern California. Unpublished report to USDA Forest Service, Pacific Southwest Region, San Francisco, California, USA.

Schneider, R. 1997. Simulated spatial dynamics of martens in response to habitat succession in the Western Newfoundland Model Forest. Pages 419–436 *in* G. Proulx, H. N. Bryant, and P. M. Woodard, editors. Martes: *Taxonomy, Ecology, Techniques and Management*. Provincial Museum of Alberta, Edmonton, Alberta, Canada.

Seglund, A.E. 1995. The use of resting sites by the Pacific fisher. M.S. Thesis. Humboldt State University, Arcata, CA, USA.

Sherburne, S.S. and J.A. Bissonette. 1993. Squirrel middens influence marten (*Martes americana*) use of subnivean access points. *American Midland Naturalist* **129**:204–207.

Simms, D.A. 1979. North American weasels: resource utilization and distribution. *Canadian Journal of Zoology* **57**:504–520.

Soulé, M.E. and J. Terborgh. 1999. *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Island Press, Washington DC, USA.

Soulé, M.E., D.T. Bolger, A.C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2**:75–92.

Sovada, M.A., A.B. Sargeant, and J.W. Grier. 1995. Differential effects of coyotes and red foxes on duck nest success. *Journal of Wildlife Management* **59**:1–9.

Spencer, W.D., R.H. Barrett, and W.J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. *Journal of Wildlife Management* **47**:1181–1186.

Stephenson, R.O., D.V. Grangaard, and J. Burch. 1991. Lynx, *Felis lynx*, predation on red foxes, *Vulpes vulpes*, caribou, *Rangifer tarandus*, and Dall sheep, *Ovis dalli*, in Alaska. *Canadian Field-Naturalist* **105**:255–262.

Strickland, M.A. 1994. Harvest management of fishers and American martens. Pages 149–164 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, USA.

Strickland, M.A., C.W. Douglas, M. Novak, and N.P. Hunziger. 1982*a*. Fisher. Pages 586–598 *in* J. A. Chapman, and G. A. Feldhamer, editors. *Wild Mammals of North America: Biology, Management, and Economics*. Johns Hopkins University Press, Baltimore, MD, USA.

Strickland, M.A., C.W. Douglas, M. Novak, and N.P. Hunziger. 1982*b*. Marten. Pages 599–612 *in* J. A. Chapman, and G. A. Feldhamer, editors. *Wild Mammals of North*

America: Biology, Management, and Eeconomics. Johns Hopkins University Press, Baltimore, Maryland, USA.

Stuewer, F.W. 1943. Raccoons: their habits and management in Michigan. *Ecological Monographs* 13:203–257.

Svendsen, G.E. 1982. Weasels. Pages 613–628 *in* J.A. Chapman, and G.A. Feldhamer, editors. *Wild Mammals of North America: Biology, Management, and Economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Szumski, M.J. 1998. The effects of mining-related metals contamination on piscivorous mammals along the upper Clark Fork River, Montana. Dissertation, University of Wyoming, Laramie, Wyoming, USA.

Taylor, S.L. and S.W. Buskirk. 1994. Forest microenvironments and resting energetics of the American marten *Martes americana*. *Ecography* 17:249–256.

Terborgh, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24:283–292.

Terborgh, J., J.A. Estes, P. Paquet, K. Ralls, D. Boyd-Heger, B.J. Miller, and R.F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39–64 *in* M. E. Soulé, and J. Terborgh, editors. *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Island Press, Washington DC, USA.

Thompson, I.D. 1986. Diet choice, hunting behavior, activity patterns, and ecological energetics of marten in natural and logged areas. Dissertation. Queen's University, Kingston, Ontario, Canada.

Thompson, I.D. 1994. Marten populations in uncut and logged boreal forests in Ontario. *Journal of Wildlife Management* 58:272–279.

Thompson, I.D. and A.S. Harestad. 1994. Effects of logging on American martens, and models for habitat management. Pages 355–367 *in* S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. *Martens, Sables, and Fishers: Biology and Conservation*. Cornell University Press, Ithaca, New York, USA.

Thurber, J.M., R.O. Peterson, J.D. Woolington, and J.A. Vucetich. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. *Canadian Journal of Zoology* 70:2494–2498.

Thurber, J.M., R.O. Peterson, T.D. Drummer, and S.A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61–68.

Todd, A.W., L.B. Keith, and C.A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. *Journal of Wildlife Management* 45:629–640.

Trapp, G.R. 1978. Comparative behavioral ecology of the ringtail and gray fox in southwest Utah. *Carnivore* 1:3–32.

Trapp, G.R. and D.L. Hallberg. 1975. Ecology of the gray fox (*Urocyon cinereoargenteus*): a review. Pages 164–178 *in* M.W. Fox, editor. *The Wild Canids*. Van Reinhold Co., New York, New York, USA.

Twining, H. and A. Hensley. 1947. The status of pine martens in California. *California Fish and Game* 33:133–137.

Tyson, E.L. 1950. Summer food habits of the raccoon in southwest Washington. *Journal of Mammalogy* 31:448–449.

USDA Forest Service and USDI Bureau of Land Management. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA.

USDA Forest Service. 1996. Status of the Interior Columbia Basin: summary of scientific findings. US Forest Service General Technical Report **PNW-GTR-385**.

USDA Forest Service. 2001. Sierra Nevada Forest plan amendment. Final environmental impact statement. Pacific Southwest Region, Vallejo, CA, USA.

Verts, B.J. 1967. *The Biology of the Striped Skunk*. University of Illinois Press, Urbana, Illinois, USA.

Verts, B.J. and L.N. Carraway. 1998. *Land Mammals of Oregon*. University of California Press, Berkeley, California, USA.

Vitousek, P. 1988. Diversity and biological invasions of oceanic islands. Pages 181–189 *in* E.O. Wilson, and F.M. Peter, editors. *Biodiversity*. National Academy Press, Washington DC, USA.

Voigt, D.R. 1987. Red fox. Pages 379–392 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resources, Ontario, Canada.

Wade-Smith, J. and B.J. Verts. 1982. *Mephitis mephitis*. *Mammalian Species* 173:1–7.

Weaver, J.L., P.C. Paquet, and L.F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* **10**:964–976.

Weckwerth, R.P. and V.D. Hawley. 1962. Marten food habits and population fluctuations in Montana. *Journal of Wildlife Management* **26**:55–74.

Weir, R.D. and A.S. Harestad. 1997. Landscape-level selectivity by fishers in south-central British Columbia. Pages 252–264 *in* G. Proulx, H.N. Bryant, and P.M. Woodard, editors. Martes: *Taxonomy, Ecology, Techniques and Management*. Provincial Museum of Alberta, Edmonton, Alberta, Canada.

White, P.J., and R.A. Garrott. 1997. Factors regulating kit fox populations. *Canadian Journal of Zoology* 75:1982–1988.

Wilcomb, M.J. 1948. Fox populations and food habits in relation to game birds in the Willamette Valley, Oregon. M.S. Thesis. Oregon State College, Corvallis, Oregon, USA.

Willey, R.B. and R.E. Richards. 1974. The ringtail (*Bassariscus astutus*): vocal repertoire and Colorado distribution. *Journal of the Colorado-Wyoming Academy of Science* 7(5):58.

Wilson, D.E. 1982. Wolverine. Pages 644–652 *in* J.A. Chapman and G.A. Feldhamer, editors. *Wild Mammals of North America*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Wisz, M.S. 1999. Islands in the Big Sky: equilibrium biogeography of isolated mountain ranges in Montana. M.S. Thesis, University of Colorado, Boulder, Colorado, USA.

Wren, C.D. 1985. Probable case of mercury poisoning in a wild otter, *Lutra canadensis*, in northwestern Ontario. *Canadian Field-Naturalist* **99**:112–114.

Wright, S. 1978. *Evolution and the Genetics of Populations*. Volume 4. University of Chicago Press, Chicago, Illinois, USA.

Wright, S.J., M.E. Gompper, and B. DeLeon. 1994. Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71:279–294.

Yeager, L.E. and W.H. Elder. 1945. Pre- and post-hunting season foods of raccoons on an Illinois goose refuge. *Journal of Wildlife Management* 9:48–56.

Zezulak, D.S. and R.G. Schwab. 1979. A comparison of density, home range, and habitat utilization of bobcat populations at Lava Beds and Joshua Tree national

monuments, California. *Bobcat Research Conference, National Wildlife Federation Scientific and Technical Series* **6**:74–79.

Zielinski, W.J. 1995. Track plates. Pages 67–86 *in* W.J. Zielinski, and T.E. Kucera, editors. American marten, fisher, lynx, and wolverine: survey methods for their detection. U.S. Forest Service, General Technical Report **PSW-157**, Albany, California, USA.

Zielinski, W.J., and T.E. Kucera. 1995. American marten, fisher, lynx, and wolverine: survey methods for their detection. U.S. Forest Service General Technical Report **PSW-157** Albany, California, USA.

Zielinski, W.J. and H.B. Stauffer. 1996. Monitoring *Martes* populations in California: survey design and power analysis. *Ecological Applications* **6**:1254–1267.

Zielinski, W.J., W.D. Spencer, and R. D. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. *Journal of Mammalogy* **64**:387–396.

Zielinski, W.J., T.E. Kucera, and R. H. Barrett. 1995. The current distribution of fisher, *Martes pennanti*, in California. *California Fish and Game* **81**:104–112.

Zielinski, W.J., R.L. Truex, C.V. Ogan, and K. Busse. 1997. Detection surveys for fishers and American Martens in California, 1989–1994: Summary and interpretations. Pages 372–394 *in* G. Proulx, H.N. Bryant, and P.M. Woodward, editors. Martes: *Taxonomy, Ecology, Techniques and Management*. Provinicial Museum of Alberta Edmonton, Canada.

Zielinski, W.J., N.P. Duncan, E.C. Farmer, R.L. Truex, A.P. Clevenger, and R.H. Barrett. 1999. Diet of fishers (*Martes pennanti*) at the southernmost extent of their range. *Journal of Mammalogy* **80**:961–971.

Zielinski, W.J., K.M. Slauson, C.R. Carroll, C.J. Kent, and D.G. Kudrna. 2001. Status of American martens in coastal forests of the Pacific states. *Journal of Mammalogy* **82**:478–490.

Mammal Community Dynamics

Management and Conservation in the Coniferous Forests of Western North America

Edited by

CYNTHIA J. ZABEL
USDA Forest Service

ROBERT G. ANTHONY
USDI Geological Survey

CAMBRIDGE
UNIVERSITY PRESS