Chapter 2

American Marten

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INTRODUCTION

Natural History

The American marten (*Martes americana*), also called the marten or American sable, is a carnivorous mammal about the size of a small house cat. Its total length is between 500 and 680 mm and it weighs 500-1400 g as an adult, depending on sex and geography (Buskirk and McDonald 1989; Strickland et al. 1982). The male is 20-40% larger than, but otherwise similar in appearance to, the female. Both sexes are furred with glossy hair of medium length, are tan to chocolate in color, and have an irregular neck or throat patch ranging from pale cream to bright amber. Its face is pointed and foxlike in shape, its torso is slender, and its legs and tail are intermediate in length and darkly furred. Each foot has five toes, all of which touch the ground, and the claws are light in color and semiretractable (Buskirk 1994; Clark and Stromberg 1987). Although its close relatives include skunks and other species with powerful scent glands, the marten, even when frightened, produces odors only weakly perceptible to humans.

The American marten is one of seven species in the genus *Martes,* within Family Mustelidae, Order Carnivora (Corbet and Hill 1986). Along with the Eurasian pine marten (*M. martes),* the sable (*M. zibellina*), and the Japanese marten (*M. melampus*), it belongs to a group of closely related species called the "boreal forest martens" (Buskirk 1992). These four species replace each other geographically from west to east across the circumboreal zone from Ireland to Newfoundland Island, and they exhibit close similarities of size, shape, and ecology (Anderson 1970). The genus *Martes* is distinguishable from other North American mustelids by the presence of four upper and lower premolars. The only other *Martes* in North America is the much larger-bodied fisher (*M. pennanti*), which occupies similar habitats but has a smaller geographic range.

The American marten is broadly distributed. It extends from the spruce-fir forests of northern New Mexico to the northern limit of trees in arctic Alaska and Canada, and from the southern Sierra Nevadas of California to Newfoundland Island (Hall 1981). In Canada and Alaska, its distribution is vast and continuous, but in the western contiguous United States, its distribution is limited to mountain ranges that provide preferred habitat.

American martens occupy a narrow range of habitat types, living in or near coniferous forests (Allen 1987). More specifically, they associate closely with late-successional stands of mesic conifers, especially those with complex physical structure near the ground (Buskirk and Powell 1994). Martens may inhabit talus fields above treeline (Grinnell et al. 1937; Streeter and Braun 1968) but are seldom or never found below the lower elevational limit of trees. In Alaska, but not elsewhere, martens have been reported to occur in early post-fire stages that have few living trees where tree boles have fallen to the ground in dense networks or where herbaceous growth is dense (Johnson and Paragi 1993; Magoun and Vernam 1986).

The diet varies by season, year, and geographic area. In summer, the diet includes bird eggs and nestlings, insects, fish, and young mammals. In fall, berries and other fruits are important foods. And in winter, voles, mice, hares, and squirrels dominate the diet. In some geographic areas, single prey species are especially important because of their high availability---for example, snowshoe hares (*Lepus americanus*) in Manitoba (Raine 1981) and deer mice (*Peromyscus maniculatus*) on Vancouver Island (Nagorsen et al. 1989). Martens hunt for small mammals by traveling on the ground or snow surface. Prey that live beneath the snow, such as voles, mice, and shrews, are caught by entering access points to the subnivean space created by coarse woody debris and other structures (Corn and Raphael 1992; Koehler et al. 1975). Martens make occasional forays into trees and have good tree-climbing abilities (Grinnell et al. 1937).

Community interactions between martens and other vertebrates are not well understood. Predation on American martens seldom is directly observed or inferred from marten remains in fecal pellets or castings. But the threat of predation is thought to be strong in shaping habitat-selection behaviors by martens (Buskirk and Powell 1994). This is in part because of documented predation on Eurasian pine martens (Brainerd 1990) and because of the strong psychological avoidance of open areas by American martens (Hawley and Newby 195'7), which is generally inferred to be an evolved response to predation threats. Predation on martens by coyotes (*Canis latrans*), red foxes (*Vulpes*) (Ruggiero, unpubl. data), and great-horned owls (*Bubo virginianus*) (Baker 1992) has been documented. Unlike martens, these species are generalists associated with a broad range of habitats including early successional. and fragmented landscapes. Martens occur locally sympatrically with various other mustelid species, but competitive interactions involving limiting resources have not been reported.

Martens tend to be shy and have been called "wilderness animals" (Thompson-Seton 1925); even people who live in marten habitat may seldom see them. However, martens occasionally seem fearless of humans and approach closely. They may be strongly attracted to human structures and human foods, so that they at times seem locally abundant and tame (Halvorsen 1961). But this impression usually is transient. Marten tracks in. snow, which are distinctive to experienced observers, follow circuitous routes over their large home ranges, staying close to overhead cover and investigating openings to the subnivean space where coarse woody debris penetrates the snow surface. Although they are agile climbers of trees and cliffs, they mostly travel on the ground (Francis and Stephenson 1972). Martens are active at various times of day and night and appear to be flexible in their activity patterns (Hauptman 1979).

In comparison with the fisher, the marten engages in more arboreal and subnivean activity (Strickland and Douglas 1987), eats smaller prey (Clem 1977), and associates more strongly with coniferous stands. Both species are similarly intolerant of vegetation types lacking overhead cover (Buskirk and Powell 1994).

American martens have been trapped for fur since aboriginal times and are primarily known as furbearers over much of their range. Their distribution has contracted and then recovered in parts of their range, but it is smaller today than at the time of European contact. Martens have been especially impacted by human activities in the Pacific Northwest.

The knowledge base for the marten in the western United States, excluding Alaska, is the strongest of the forest carnivores considered in this assessment (table 1).

Current Management Status

Neither the American marten nor any of its local populations are protected under the Endangered Species Act. Likewise, as of 15 July 1991, this species had not been listed in any appendices to the Convention on International Trade in Endangered Species of Wild Flora and Fauna, or in the International Union for the Conservation of Nature and Natural Resources Red List of Threatened Animals (Wilson and Reeder 1993). In most state and provincial jurisdictions in western North America where it occurs, the American marten is managed as a furbearer (Appendix C, table 4a). This management generally allows martens to be taken by trap, but not by firearm, and involves the use of one or more of the usual measures: licensing of trappers, seasonally closed, requirements that pelts or carcasses be submitted for sealing inspection, and assignment or registration of traplines (Appendix C, table 4a; Strickland and Douglas 1987). In five western state jurisdictions (California, Nevada, New Mexico, South Dakota, and Utah) martens may not be legally taken in any area of the jurisdiction at any time. California classifies the marten as a furbearer but has had no open season since 1952. Only two other states have given the marten a formal listing: "Protected" in Utah and "Endangered, Group II" in New Mexico.

Several federal land management agencies in the western conterminous states, representing a range of jurisdictional powers, assign special management status to the marten. Pursuant to the National Forest Management Act of 1976 and 36 CFR Ch. II, Part 219.19 a. 1., many forest plans in Regions 1, 2, 4, 5, and 6 of the National Forest System have designated the marten as an ecological indicator species (e.g., Gallatin National Forest) or a "high-interest species" (e.g., Wasatch-Cache National Forest). These special designations are listed in Appendix C. Regions 2 and 5 have placed the marten on their regional foresters' "sensitive species" lists. Sensitive species are those for which continued persistence of well-distributed populations on National Forest System lands has been identified as a concern.

Other regulations or agency policies are not specific to martens but affect their conservation; for example, trapping is prohibited in most units of the National Park System. Also, trapper access is decreased, and de facto partial protection provided, by prohibitions of motorized travel in Research Natural Areas on National Forests and in wilderness areas established pursuant to the Wilderness Act of 1964.

DISTRIBUTION AND TAXONOMY

Distribution

Anderson (1970, 1994) reported that the American marten came to North America by way of the Bering Land Bridge during the Wisconsin glaciation, which ended about 10,000 years ago. During the Wisconsin, martens extended much farther south and lower in elevation than they do today (Graham and Graham 1994), occurring in what is now Alabama. The current geographic range is temperate to arctic and spans the continent from east to west, including offshore islands (Hall 1981). The main part of the distribution comprises the boreal and taiga zones of Canada and Alaska. South of this vast area, the distribution becomes insularized, with fingers and islands following western mountain ranges south-

Table 1.-The knowledge base for American martens in the western United States, excluding Alaska, by subject. This includes studies for which the subject was a specific objective of the study; incidental observations are not included. Sample size is number of animals studied, or for food habits, number of scats or gastrointestinal tract contents, unless stated otherwise. Sample sizes for dispersal include only juveniles. Theses and dissertations are not considered separately from reports and publications that report the same data. A total of 26 studies (*) are represented in this table, discounting redundancies.

Topic, author	Location	Method	Duration	Sample size
Home range & habitat use				
*Burnett 1981	NW Montana	Telemetry(hr)[1]	18 mo.	11
*Buskirk et al. 1989	SE Wyoming	Telemetry	2 winters	8
*Campbell 1979	NW Wyoming	Telemetry(hr)	15 mo.	4
		Marking		17
*Clark 1984	NW Wyoming	Marking	18 mo.	5
*Corn and Raphael 1992	S Wyoming	Searches	3 mo.	43 subnivean access sites
*Fager 1991	SW Montana	Telemetry(hr)	<1 yr.	7
		Marking		37
*Hargis 1981	C California	Snow-tracking	2 winters	35 km of tracks 2-5 martens
*Hauptman 1979	NW Wyoming	Telemetry(hr)	12 mo.	4
*Hawley 1955	NW Montana	Marking(hr)	21 mo.	69
*Koehler and Hornocker 1977	Idaho	Marking	7 mo.	13
		Snow transects		255 track observations
*Koehler et al. 1990	N Washington	Snow transects	4 mo.	11 track observations
*Martin 1987	N California	Telemetry	28 mo.	210 resting sites, 10 individuals
*Newby 1951	Washington	Marking	36 mo.	4
*Sherburne and Bissonette 1993	NW Wyoming	Searches	8 mo.	70 subnivean access sites
Home range & habitat use				
*Simon 1980	N California	Telemetry(hr)	16 mo.	8
*Spencer 1981	N California	Marking	15 mo.	14
		Telemetry(hr)		4
*Wilbert 1992	S Wyoming	Telemetry	14 mo.	190 resting sites, 11 individuals
Demography				
Campbell 1979	NW Wyoming	Marking	15 mo.	17
Clark 1984	NW Wyoming	Marking	18 mo.	39
Fager 1991	SW Montana	Marking	12 mo.	37

(*Continued*)

Table 1.-(continued).

Topic, author	Location	Method	Duration	Sample size
Hauptman 1979	NW Wyoming	Marking	12 mo.	20
Hawley 1955	NW Montana	Marking	21 mo.	69
*Jonkel 1959	NW Montana	Marking	10 mo.	161
*Marshall 1948	Idaho	Carcass	36 mo.	124
Simon	N California	Marking	16 mo.	18
*Weckwerth 1957	NW Montana	Marking	12 mo.	45
Food habits				
Campbell 1979	NW Wyoming	Scats	4 mo.	145
*Gordon 1986	Colorado	G. I. tracts	6 mo.	32
Hargis	C California	Scats	2 winters	91
Hauptman 1979	NW Wyoming	Scats	12 mo.	233
Food habits				
Koehler and Hornocker 1977	Idaho	Scats	7 mo.	129
*Marshall 1946	NW Montana	Scats	1 winter	46
Marshall 1948	Idaho	Scats	36 mo.	19
		G.I. tracts		20
Martin	N California	Scats	28 mo.	100
*Murie	NW Wyoming	Scats	Multi-year	528
Newby	Washington	Scats	3 mo.	95
		G. I. tracts	11 mo.	17
*Remington 1951	Colorado	Scats	15 mo.	198
Sherburne 1993	NW Wyoming	Scats	8 mo.	69
Simon	N California	Scats	16 mo.	99
Weckwerth 1957	NW Montana	Scats	12 mo.	561
*Zielinski 1981	N California	Scats	15 mo.	428
Dispersal				
Burnett	NW Montana	Telemetry	18 mo.	6
Jonkel	NW Montana	Marking	10 mo.	11
Natal dens				
*Ruggiero, in review	S Wyoming	Telemetry	72 mo.	14 natal dens, 6 females

[1] *hr = home range size reported*

ward. The southern limit of distribution of martens coincides roughly with that of coniferous tree species, for example *Picea engelmannii* in the southern Rocky Mountains, that develop stand conditions with which martens associate (c.f. Hall 1981 and Little 1971, Map 37-W).

The distribution of the American marten has undergone regional contractions and expansions, some of them dramatic. On balance, the American marten has a smaller distribution now than in presettlement historical times (Gibilisco 1994); the total area of its geographic range appears similar to that early in this century, when it was at its historical low. American martens have reoccupied much of southern New England with the aid of transplantation after being absent for much of the 1900's. Farther to the northeast, however, martens have undergone numerical and distributional declines (Thompson 1991). Martens are endangered or extinct in mainland Nova Scotia, and on Newfoundland, Prince Edward, and Cape Breton Islands (Bergerud 1969; Dodds and Martell 1971; Gibilisco 1994; Thompson 1991). The status of martens in the maritime provinces has been attributed to the logging of late-successional coniferous forests and to trapping for fur (Bissonette et al. 1989; Thompson 1991). Consistent with this, the expansion of the range of martens in southern New England is thought to be related to forest succession that has taken place there for about the last century (Litvaitis 1993). Martens were lost from large areas of the north-central United States during the late 1800's and early 1900's, primarily as a result of forest loss (Berg and Kuehn 1994) to logging and agriculture. Since about 1930. the range of martens in this region has slowly expanded as forests succeeded to conifers. The marten is now extirpated from seven states where it occurred historically: North Dakota, Illinois, Indiana, Ohio, Pennsylvania, New Jersey, and West Virginia (Clark et al. 1987; Thompson 1991).

In the Shining Mountains, Northern Rocky Mountain Forest, Utah Rocky Mountains, and Colorado Rocky Mountains ecoprovinces, (Appendix A), distributional changes have apparently been of small scale. Only the Tobacco Root Mountains of Montana reportedly have lost an historically present marten population (Gibilisco 1994). In the Georgia-Puget Basin, Pacific Northwest Coast and Mountains, and Northern California Coast Ranges ecoprovinces, (Appendix A), distributional losses have been major. Martens now are scarce or absent in the coast ranges of northern California, where they were once common. Evidence for this loss is provided by the near complete absence of marten sightings from the coast ranges since 1960 (Schempf and White 1977) compared to the early part of this century (Grinnell et al. 1937). This apparent range reduction involves parts of Humboldt, Del Norte, Mendicino, Lake, and Sonoma Counties, and it corresponds closely to the distribution of *M. a. humboldtensis,* a subspecies recognized by both Hall (1981) and Clark et al. (1987). Therefore, this apparent loss may jeopardize a named taxon, the Humboldt marten. Because trapping has been illegal in California since 1953, and because marten sightings in northwestern California have decreased rather than increased during this period of protection, trapping could not have accounted for the decline in marten numbers in northwestern California in the last 40 years. Therefore, loss of late-successional forest to logging must be considered the most likely cause.

Some range expansions have occurred through transplantation of martens, but other transplants have only hastened range expansions that were occurring naturally (Slough 1994). Still others were attempted to populate vacant habitat but have failed to produce persistent populations (Berg 1982; Slough 1994). Areas that currently have marten populations established by transplantation include Baranof, Chichagof, and Prince of Wales Islands in Alaska (Burris and McKnight 1973; Manville and Young 1965) and the Black Hills of South Dakota (unpubl. data in Fredrickson 1981). Translocation has proven an effective conservation tool if sufficient numbers of animals are translocated, and if quantity and quality of habitat at the release site are adequate (Slough 1994).

Taxonomy

All systematic studies of this species have been based on morphology, especially skull and dental measurements; no biochemical studies of phylogeny have been completed to date. In the first half of this century, the American marten was classified as from two (Merriam 1890) to six species (Miller 1923), but today it is considered a single species (*Martes americana*) (Clark et al. 1987; Hall 1981). Up to 14 subspecies have been recognized (Hall and Kelson 1959), but Hagmeier (1958,1961) and Anderson (1970) considered these distinctions arbitrary, and Clark et al. (1987) recognized only eight subspecies in two "subspecies groups." The "caurina" subspecies group includes those (*M. a. caurina, humboldtensis, nesophila*) in the Rocky Mountains, Sierra Nevada, and the coastal Pacific states. The "americana" subspecies group includes all other subspecies (*M. a. abietinoides, actuosa, americana, atrata, kenaiensis*). Only two of the eight subspecies recognized by Clark et al. (1987) were separated from others by geographic barriers in presettlement times: *M. a. nesophila,* on the Queen Charlotte Islands, British Columbia, and the Alexander Archipelago; and *M. a. atrata,* on Newfoundland Island. The others intergrade with each other along lengthy zones of subspecies contact.

Population Insularity

Our knowledge of isolated populations is almost certainly incomplete and may not include important natural or human-caused cases. Population insularity can only be inferred because true insularity results from a lack of movement among populations, and the absence of movements is impossible to prove.

Martens occur or occurred on several ocean islands that were connected to the mainland during the Wisconsin glaciation. These include Vancouver, Graham, and Moresby Islands off the coast of British Columbia, and Mitkof, Kupreanof, and Kuiu Islands in southeast Alaska (Alaska Department of Fish and Game, unpubl. data; Hall 1981). In the Atlantic, these include Newfoundland, Anticosti, Prince Edward, and Cape Breton Islands (Gibilisco 1994; Hall 1981). In addition, martens occupy several islands in the Alexander Archipelago, including Baranof, Chichagof, and Prince of Wales Islands, to which they were introduced in 1934, 1949-52, and 1934, respectively (Alaska Department of Fish and Game, unpubl. data; Burris and McKnight 1973; Manville and Young 1965).

Examples of insular populations on the mainland are more difficult to identify, partly because the dispersal abilities of martens on land are more subject to interpretation than are their abilities across water. Still, biologists are generally agreed that over 5 kilometers of treeless land below the lower elevational limit of trees acts as a complete barrier to dispersal (Gibilisco 1994; Hawley and Newby 1957). On this basis, several mainland populations can be identified that likely have been isolated since late Pleistocene or early Holocene times. These include the Bighorn Mountains in north-central Wyoming (Clark et al. 1987) and the Crazy Mountains, Big Belt Mountains, and Little Belt Mountains in Montana (Gibilisco 1994). The Bighorn Mountains are separated from other populations to the northwest by arid shrublands along the Bighorn River. Martens occurred in the isolated Tobacco Root Mountains in Montana in historical times but now are apparently extinct (Gibilisco 1994). Martens in Colorado, New Mexico, and southern Wyoming are well isolated from those in the northern Rockies by the Green River-Wyoming Basin complex, an important zoogeographic barrier for other boreo-montane mammals as well (Findley and Anderson 1956). Cary (1911) identified a potentially isolated population on the eastern White River Plateau of Colorado.

These naturally isolated marten populations in the montane southern part of the range result from several interacting processes. The coniferous forests to which martens are now limited are high-elevation relicts of more extensive forests that existed during the late Pleistocene (Wright 1981) but have since contracted. Today's montane boreal forests are surrounded by low-elevation, nonforested lands, which are complete barriers to marten dispersal (see Habitat section). Because of these barriers martens are not likely to have reached the montane islands, even over millennia. Therefore, these isolated populations are believed to have persisted since late Pleistocene or early Holocene time. Some mountain ranges that lack extant populations of martens have yielded fossil or subfossial remains of this species, providing insight to the prehistoric distribution (Graham and Graham 1994; Patterson 1984). The persistence of some isolated marten populations, and the extinction of others, suggests the importance of sufficient habitat that can support populations large enough to outlast the processes that push small populations toward extinction. These processes include inbreeding, genetic drift, Allee effects, and stochastic events (Gilpin and Soulé 1986). Inbreeding refers to matings among closely related individuals, which is inevitable in small populations. Drift refers to random changes in allele frequencies in small populations resulting from random sampling during gametogenesis and syngamy. Allee effects result from low probabilities of animals finding mates at very low densities. Stochastic events are more or less unpredictable environmental conditions that affect size or structure of populations.

Lastly, some parts of the distribution of martens appear to have been isolated from others by human-caused habitat fragmentation. These include the isolation of martens on the Olympic Peninsula from those in the Cascades (Sheets 1993) and the isolation of martens in western California and Oregon, if they still exist, from those farther north (c.f. Clark et al. 1987; Gibilisco 1994; Hall 1981). In addition, the marten population in the Blue Mountains of southeastern Washington and northeastern Oregon likely now is isolated from that in the mountains east of the Snake River (Gibilisco 1994).

Management Considerations

1. The marten has undergone an apparent range reduction in northwestern California that may threaten the Humboldt marten, *M. a. humboldtensis.* This reduction likely is attributable to loss of habitat through the cutting of late-successional forest.

2. The geographic distribution of martens in Washington, Oregon, and northwestern California has been dramatically reduced. This reduction likely is attributable to loss of habitat through the cutting of late-successional forest.

3. Several populations in the western United States are known or hypothesized to be isolated. Insularity decreases population persistence times relative to those of otherwise similar populations that receive episodic ingress (Diamond 1984). Therefore, isolated populations may be especially vulnerable to human actions, particularly where the population is small and the carrying capacity of the habitat is reduced. Special management consideration, including maintenance of the carrying capacity of the habitat, must be given to these populations.

4. Known isolated populations include some that have persisted since prehistoric times, others that have been created by human-caused fragmentation of formerly contiguous habitat, and still others that

have been established by transplantation. Populations that have persisted since prehistoric times likely represent locally adapted forms and warrant greater protection than those created by transplant.

5. Martens are apparently extinct in some isolated habitats where they occurred in historical times. Special management approaches, including transplantation, may be appropriate for these areas.

6. Logging is commonly regarded as the primary cause of observed distributional losses in historic times in the western contiguous United States. Fire, insects, and disease are other important causes of tree death in the western conterminous United States, but the effects of these disturbances on martens have been studied little. Because logging is unique among these disturbances in removing boles from forests, and because of the importance of boles in contributing physical structure to habitats, logging likely is more deleterious to habitat quality for martens than other disturbances. Trapping has contributed to distributional losses in other areas, including the north-central states and eastern Canada.

Research Needs

1. Develop better methods for monitoring marten populations, including presence or absence, relative abundance, and components of fitness. More reliable knowledge is needed regarding the current distribution of martens in the western United States, especially in the Pacific States and the southern Rocky Mountains.

2. Investigate systematic relationships among populations, especially those that are partially or completely isolated, in order to recognize locally adapted forms or taxonomically recognizable groups. This could also provide site-specific knowledge of rates of genetic exchange.

3. We need information about the factors that affect persistence of isolated populations. Specifically, we need knowledge of how duration of isolation, population size and demography, and variation in these attributes affect persistence.

4. Extant populations isolated from other populations by water or land present an opportunity to examine population persistence in relation to area, habitat characteristics, and duration of isolation. Knowledge of these will improve our ability to address the dependency of marten populations on mesic coniferous forests (Ruggiero et al. 1988).

POPULATION ECOLOGY

Demography

Most females first mate at 15 months of age and produce their first litters at 24 months (Strickland et al. 1982). For mammals, this is a prolonged time to sexual maturity. Taylor's (1965) allometric equation for mammals gives a predicted maturation time for a 1-kg mammal of 5 months. But even yearling females, up to 78% in some studies (Thompson and Colgan 1987), can fail to produce ova. Females ≥2 years also may not ovulate, with pregnancy rates as low as 50% in years of environmental stress (Thompson and Colgan 1987). The course of spermiation in relation to age has not been studied.

Among 136 litters reviewed by Strickland and Douglas (1987), the mean size was 2.85, and the range 1-5. This litter size is about that expected on the basis of body size; allometric equations by Sacher and Staffeldt (1974) and Millar (1981) predict litter sizes for a 1-kg mammal of 2.5-3.0. There is some evidence of age-dependent litter size, with a peak at about 6 years, and senescence at >12 years (Mead 1994). Breeding can occur at ages up to 15 years (Strickland and Douglas 1987). A maximum of one litter is produced per year, compared with an allometrically predicted litter frequency for a 1-kg mammal of 1.4 /year (Calder 1984). By multiplying litter size by litter frequency, Calder (1984) expressed natality rate for terrestrial placental mammals as a function of body size; a 1-kg mammal is expected to produce 3.4-3.9 offspring/year. By this standard, the yearly reproductive output of pregnant female martens (mean = 2.9) is low.

Longevity statistics depend heavily on whether the population is captive, wild and trapped, or wild and untrapped (Strickland and Douglas 1987). Captive martens as old as 15 years and a marten 14.5 years of age from a trapped wild population have been reported (Strickland and Douglas 1987). This is high, by mammalian standards; the allometric equation developed by Sacher (1959) predicts maximum longevity for a 1-kg mammal of 11.6 years. Therefore, American martens are long-lived. However, these figures say little about the life expectancy of newborn martens in the wild. For 6,448 trapped martens from the Algonquin region of Ontario, Strickland and Douglas (1987) reported a median age for both males and females of <1 year. These data suggest the young age at which martens in trapped populations die.

The age structure of wild populations depends heavily on whether the population is trapped. Among trapped populations, trapping commonly is the primary mortality source, causing up to 90% of all deaths (Hodgman et al. 1993). Fager (1991) reported that 27-100% of marked martens in his three study areas in southwestern Montana were caught by fur trappers during one trapping season. In spite of the high proportion of young animals in trapped samples, heavy trapping over several years tends to selectively remove old animals and skews age structures toward young animals (Strickland and Douglas 1987; Strickland et al. 1982). As a result, structures of trapped populations respond mostly to timing and intensity of harvest. Harvested populations are affected by resources such as prey populations only when the resources fall to levels below those that can support the low marten numbers maintained by trapping (Powell 1994). At the same time, Powell (1994) pointed out that single-year recruitment responses to high or low prey abundance can be reflected in age structure for years to come.

Sex structure likewise is difficult to infer from data from trapping, because of its inherent sampling biases. Males are more likely than females to be taken by trapping (Buskirk and Lindstedt 1989), so that trapped samples show a higher proportion of males than is in the population. As a result, populations subjected to high trapping mortality usually are skewed toward females. Still, live-trapping studies have inferred population sex ratio by comparing numbers of animals captured, by sex, with the numbers of captures of those animals, by sex. Males tend to exhibit more captures per individual caught than do females. Archibald and Jessup (1984) showed that the ratio of males to females in their study population did not differ from 1, whereas fur trappers from their area captured predominantly males. Powell (1994) predicted that even sex ratios would be the general case for untrapped populations.

Ecological Influences on Population Size and Performance

Food availability gives the best evidence of ecological influences on population attributes. Weckwerth and Hawley (1962) reported a decrease of about 30% in numbers of adult martens, and of about 80% in numbers of juvenile martens, over a 3-year period when small mammal numbers dropped about 85%. Likewise, Thompson and Colgan (1987) reported a decline in marten numbers in uncut forest of about 85% in the face of a synchronous decline in prey biomass estimated at over 80%. Thompson and Colgan (1987) also found that food shortage had a stronger effect on resident males than on females, whereas Weckwerth and Hawley (1962) observed effects on both resident males and females. Thompson and Colgan (1987) also observed food-shortage effects on pregnancy rate, ovulation rate, age structure, and home-range size. This phenomenon could be important in conservation strategies, because in some forest types, dramatic fluctuations in the marten prey base have been documented (Nordyke and Buskirk 1991; Weckwerth and Hawley 1962). This could represent a special concern as a stochastic influence on the persistence of small or isolated populations.

Hénault and Renaud (in press) examined the relationship between body condition of martens in Quebec and the relative proportions of deciduous and coniferous forest where they lived. They found a positive relationship between the weights of martens and the coniferous component of their habitat. They inferred that coniferous habitats conferred better body condition on martens than did deciduous-dominated habitats.

Strickland et al. (1982) reported various endoparasites and an incidence rate of 11% for toxoplasmosis, and 1.4% for Aleutian disease, but pointed out that none of these has ever been found to be a substantive mortality source for martens. Zielinski (1984) reported that about one-third of the martens he sampled had been exposed to plague, but he noted no deaths, even among the animals with the highest antibody titers. Fredrickson (1990), however, observed a dramatic die-off of martens on Newfoundland Island, which he attributed to canine distemper.

Population Sizes and Trends

Densities of marten populations have been estimated mostly by attempts at exhaustive trapping and marking, or by telemetry. These estimates do not assure that all martens in a study area are detected; therefore the estimates should be considered conservative. Francis and Stephenson (1972) estimated the density of martens in their Ontario study area to be 1.2-1.9/km^2. Also in Ontario, Thompson and Colgan (1987) estimated the density of martens to vary from 2.4/km^2 in the fall of a year of prey abundance to 0.4/km^2 in the spring of a year of prey scarcity.

Archibald and Jessup (1984) estimated the fall density of resident adults in their Yukon study area to be 0.6/km^2, the same as that found by Francis and Stephenson (1972). Soutiere (1979) reported the density of adult residents to be 1.2/km^2 in undisturbed and selectively cut forest but only 0.4/km^2 in clearcut forest. These values show some consistency across geographic areas and are remarkably low, even by comparison with other mammalian carnivores, which tend to occur at low densities. Peters (1983:167) showed that, for terrestrial carnivores, population density scales to the -1.46 exponent of body mass; so a 1-kg carnivoran is expected to occur at a population density of 15/km^2. The observed densities of American marten populations are about one-tenth of this. Therefore, martens occur at very low densities by carnivoran standards, and even lower densities if compared to mammals generally.

Even unharvested marten populations undergo marked changes in density. In addition to the six-fold fluctuation reported by Thompson and Colgan (1987), Weckwerth and Hawley (1962) reported a four-fold change in density in Montana. Indeed, one of the goals of managing trapped populations is to decrease population fluctuations (Powell 1994), which may have important implications for habitat relationships and dispersal.

Few data sets allow evaluation of population trends over long periods, and this dearth of data is a serious constraint on conservation planning. Data on harvests for furbearers are notoriously sensitive to fur prices (Clark and Andrews 1982), and data on catch per unit effort are gathered by few if any jurisdictions. Several methods of population monitoring have been tried with martens, involving measurement scales from presence-absence (Jones and Raphael 1993) to ordinal (Thompson et al. 1989) and ratio (Becker 1991) estimators. Ordinal and ratio-scale population estimation remain largely the province of research. Detection methods summarized by Raphael (1994) include tracks in snow (Becker 1991), smoked track plates (Barrett 1983), and baited camera stations (Jones and Raphael 1993).

Direct Human Effects

Trapping is the most direct avenue by which humans affect marten populations. Because of the effects described above, populations trapped at intermediate intensities are characterized by lower densities, a predominance of females, and altered age structures relative to populations under untrapped conditions (Powell 1994; Strickland and Douglas 1987; Strickland et al. 1982). However, the effects of trapping on demography are strongly influenced by the timing of harvest. Early season trapping tends to selectively remove juveniles, but seasons that extend into late winter or spring begin to remove more adults. Likewise, early trapping tends to selectively remove males, but trapping after the onset of active gestation shifts toward selective removal of females. Direct human effects on marten populations also include highway accidents (Ruggiero, unpubl. data).

Metapopulations

Metapopulation structure implies an arrangement of populations that collectively persists, with individual units that undergo episodic extinction and recolonization (Brussard and Gilpin 1989). No such metapopulations of martens have been described, but their existence in the western United States is plausible, especially where patches of high-quality habitat are separated by habitat that is traversed by dispersing animals only at infrequent but ecologically meaningful intervals. Using metapopulation concepts to plan for conservation of martens has merit; however, we need far more information on dispersal attributes for martens, and these data are scarce.

Population Genetics

Only one study has examined genetic variability of American martens. Using allozyme electrophoresis, Mitton and Raphael (1990) found high variability in a population in the central Rocky Mountains, with 33% of the loci examined showing some variability, and a mean multi-locus heterozygosity of 0.17. Mean multi-locus heterozygosity reported by Kilpatrick et al. (1986) for terrestrial carnivorans was 0.01. But the sample size for the Mitton and Raphael (1990) study was small ($n = 10$), which may explain the large heterozygote surpluses relative to Hardy-Weinberg predictions. The lack of more complete knowledge of population genetics means that there is little basis for evaluating genetic variability of populations in relation to conservation status. Genetic data also could provide useful insights into relatedness and rates of genetic exchange among populations.

Effective population size (N_e) is a conceptualization of how a real population should be affected by inbreeding and genetic drift relative to an idealized population (Crow and Kimura 1970). Neither N_e nor N_e/N (where N is population size) has been estimated for any marten population. Calculating inbreeding N_e requires knowledge of any of several demographic and life-history traits, including population sex ratio, variation in population size over time, and among-individual variation in lifetime reproductive output (Crow and Kimura 1970; Chesser 1991). Few of these attributes are available for marten populations. Importantly, the effect of trapping-induced sex ratios biased toward females on N_e/N has not been considered for any trapped population.

Management Considerations

1. Population densities of martens are low, for their body size, in comparison with mammals or terrestrial carnivores. But, because martens are the smallest-bodied of the forest carnivores reviewed herein, their densities are higher than those of most other forest carnivore species. Assuming; habitats of similar quality, marten populations typically will be smaller than those of similar-sized other mammals but larger than those of the other forest carnivores considered in this assessment.
2. Marten populations can undergo fluctuations in size of up to an order of magnitude in response to resource conditions. These responses can be attributed to prey conditions and to loss of physical structure.
3. The reproductive rates of martens are low, and longevity is high, by mammalian standards. This suggests that, for a 1-kg mammal, martens are slow to recover from population-level impacts.
4. Some western states allow martens to be trapped each year, which may limit the ability of these marten populations to respond to resource abundance. The structure of trapped populations is altered by the persistent application of trapping mortality. The result is that marten population size and structure may reflect conditions other than habitat or prey.

Research Needs

1. To parameterize a model of population persistence, we need to know how the major vital rates vary among individuals, sexes, ages, years, and geographic areas.
2. We need multiple estimates of the size of individual populations to evaluate the reliability of currently used indices of abundance.
3. To estimate inbreeding N_e, it is necessary to know how fitness varies among individuals in a population, and how spatial patterns of mating differ from those based on distances among potential partners. The factors that enter into various estimates of N_e include sex ratio among breeders (Crow and Kimura 1970), mean number of and variance in successful matings by males, incidence of multiple paternity (Chesser 1991), and pregnancy rates and litter sizes, and variances thereof, of females by age (Chesser 1991). To calculate inbreeding N_e, it is also necessary to know how population size varies over time (Crow and Kimura 1970).
4. The genetic attributes of marten populations have been studied little. There is a need to know how population history, including size and degree of isolation, affects genetic variability. This will enable us to understand whether any extant populations exhibit the loss of genetic variability that theoretically accompanies small population size and insularity (Balls et al. 1986).
5. We also need to understand the sensitivity of martens to inbreeding -- that is, to what extent and at what level inbred martens show loss of fitness. This is important for understanding at what sizes marten populations can be expected to exhibit the behavior of extinction vortices (Gilpin and Soule 1986).

REPRODUCTIVE BIOLOGY

Phenology

Breeding occurs from late June to early August, with most matings in July (Markley and Bassett 1942). During this time, the testes become enlarged and sperm can be found in the epididymides (Jonkel and Weckwerth 1963). Females entering estrus exhibit swelling of the vulva and cytological changes that are typical of, mustelids (Enders and Leekley 1941). It is unclear whether females undergo a single long estrus or multiple brief estruses in the wild. Copulation occurs on the ground or in trees, and is prolonged (Henry and Raphael 1989; Markley and Bassett 1942). Captive females mate with multiple males (Strickland et al. 1982), and wild females likely do as well, but it is not known whether these multiple matings result in litters of multiple paternity. Ovulation is presumed to be induced by copulation (Mead 1994), but among *Martes* this has only been shown for the sable. The oocyte is fertilized in the oviduct and moves to the uterine horn, where the conceptus increases in size to that of a blastocyst, which is about 1 mm in diameter (Marshall and Enders 1942).

Like many other Carnivora, the marten undergoes embryonic diapause. The total gestation period is 260-275 days (Ashbrook and Hansen 1927; Markley and Bassett 1942), but during only the last 27 days is gestation active (Jonkel and Weckwerth 1963). Implantation of the blastocyst in the endometrium, which marks the onset of active gestation, is under photoperiodic control (Enders and Pearson 1943). Active gestation is accompanied by development of the mammaries (Mead 1994).

Parturition occurs in March and. April (Strickland et al. 1982). Newborn kits weigh about 28 g, open their eyes at about 35 days, and eat solid food beginning at about 40 days (Ashbrook and Hansen 1927). Weaning occurs at about 42 days (Mead 1994), which is late by mammalian standards. Allometric equations developed for mammals predict ages at weaning for a 1-kg mammal of from 28 days (Millar 1977) to 34 days (Blaxter 1971). Young martens emerge from the dens at about 50 days but may be moved among dens by the mother earlier (Hauptman 1979, Henry and Ruggiero, in press). The young leave the company of their mother in late summer but disperse later (Strickland et al. 1982).

Den Sites

Two types of dens are recognized in the literature: natal dens, in which parturition takes place, and maternal dens, which are occupied by the mother and young but are not whelping sites (Ruggiero, in review). A variety of structures are used for dens, with trees, logs, and rocks accounting for 70% of the reported den structures (table 2). In virtually all cases involving standing trees, logs, and snags, dens were found in large structures that are characteristic of late-successional forests (Ruggiero, in review). In Wyoming, den sites having well-developed characteristics of old-growth forest were preferred by martens, and natal den sites had significantly better-developed old-growth characteristics as compared to maternal den sites (Ruggiero, in review). Old growth was defined in this study in terms of canopy cover, number of tree species, total canopy cover, number of canopy layers, tree diameters, snag densities and diameters, and log densities and diameters. Given the importance of natal dens to recruitment, the availability of structurally complex sites could have important implications for conservation.

Mating Systems and Behavior

The marten generally displays a promiscuous breeding system, but the impregnation of multiple females by a single male, or breeding with multiple males in a single year by a female in the wild, has not been proven. As with other polygynous Carnivora (Sandell 1989), male martens are alleged to

Table 2.-Summary of den structures used by American martens (grand total = 116).

			Den structures									
Author	Location	Year	Trees	Middens	Logs	Human made	Rocks	Ground	Snags	Rootwad	Stump	Logpiles
Grinnell et al.	California	1937	1									
Remington	Colorado	1952					1					
Francis	Ontario	1958			1		1					
More	Northwest Territory	1978						1				
Hauptman	Wyoming	1979	7		2							
O'Neil	Montana	1980					1					
Simon	California	1980									1	
Burnett	Montana	1981							1			
Wynne & Sherburne	Maine	1984	4		2							
Vernam	Alaska	1987						1				
Jones & Raphael	Western Washington	1991	4						1			
Baker	British Columbia	1992								1	3	3
Ruggiero	Wyoming	in review	11	3	23	2	22	1	17			1
Total			27	3	28	2	25	3	19	1	4	4

set home range size in part to gain, access to multiple female mates (Powell 1994).

Modes of Communication

Several vocalizations have been described (Belan et al. 1978), ranging from a "chuckle" to a "scream." Martens vocalize during copulation (Henry and Raphael 1989; Ruggiero and Henry 1993) and when frightened by humans (Grinell et al. 1937) but ordinarily use vocal communication little. The role of specific vocalizations is poorly understood. Martens have a broad range of known and hypothesized means for transmitting chemical signals. These include the products of their anal sacs, abdominal glands (Hall 1926), and plantar foot glands (Buskirk et al. 1986), as well as urine and feces. But, as with vocalizations, the functions of these specific scent modalities in reproduction or other life functions are not known.

Parental Care

Maternal care includes finding a suitable natal den, carrying nest material to the den, moving kits to other dens (Henry and Ruggiero, in press; Wynne and Sherburne 1984), post-partum grooming and nursing (Brassard and Bernard 1939; Henry and Ruggiero, in press), and bringing food to the young until they are old enough to forage for themselves. Paternal care of young has not been reported and likely does not occur (Strickland and Douglas 1987), consistent with the pattern for polygynous Carnivora (Ewer 1973).

Survival of Young

Almost no data are available on survival of young to specified ages. To gather these data, newborn kits would have to be tagged or radiocollared in natal dens and tracked for the time interval of interest. This has not been done, and it is unlikely to be done in the foreseeable future. Thus, estimates of survival for the first six months of life will continue to be inferred from numbers of placental scars, which are taken to represent numbers of neonates.

Management Considerations

1. The phenology of reproductive events is important in managing harvested populations. Trapping seasons are set in part to avoid periods of breeding and maternal care of young.

2. The mating system has important implications for managing trapped populations. The predisposition of males to be caught in traps results in sex ratios favoring females. Males, however, can impregnate multiple females, so that sex ratios skewed toward females do not necessarily reduce pregnancy rates.

3. Natal den sites appear to be in very specific habitat settings and may represent a special habitat need. The availability of special habitat conditions for natal denning may limit reproductive success and population recruitment.

Research Needs

1. Obtain more reliable information on reproductive rates and variation in reproductive rates of free-ranging martens. Environmental factors, including habitat type and prey availability, that influence reproduction need to be quantitatively understood. We also need to know whether and when skewed sex ratios affect pregnancy rates in trapped populations.

2. Investigate how the loss of genetic variability that results from persistently small population size affects reproduction in martens. Reproductive dysfunction is a common correlate of inbreeding in mammals generally (Balls et al. 1988) and in mustelids (Ballou 1989) and needs to be understood better in martens.

3. Determine the natal and maternal den requirements of martens. Specifically, we require knowledge of how habitat needs for reproduction affect reproductive success, and whether these habitat needs are more or less limiting than habitat needs for other life functions.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

General Foraging Ecology and Behavior

About 22 published studies have reported diets of American martens (Martin 1994), and most authors have considered the marten a dietary generalist (Simon 1980; Strickland and Douglas 1987). Martens kill vertebrates smaller and larger than themselves, eat carrion, and forage for bird eggs, insects, and fruits (table 3). Martens are especially fond of human foods but seldom are implicated in depredation on domestic animals or plants (Buskirk 1994).

Martens forage by walking or bounding along the ground or snow surface, investigating possible feed

Table 3.-Major food items in the diet of American marten. Values given are percent frequency of occurrence for all seasons sampled.

Location	Number of scats	Cricetids (except muskrat)	Shrews	Sciurids	Snowshoe hares	Ungulates	Birds	Fruits	Insects	Human foods
Maine[1]	412	~80	7.0	~7	1.7	0.7	18.0	•	8.3	•
Northwest Territories[2]	499	89	~6	6	5	0	19	~23	~14	•
Sierra Nevadas California[3]	300	~20	2.2	•	4.9	1.2	8.8	~5	8.0	6.0
Northwest Territories[4]	172	>90	1.2	0	0	•	•	•	32	•
Western Montana[5]	1758	73.7	7.6	12.0	2.9	4.7	12.0	29.2	19.0	•
Alberta[6]	200	66.0	1.6	10.2	1.6	<1	4.3	5.2	5.2	•
Interior Alaska[7]	466	73	0	<1	<1	<1	10	17	0	•
Northern Idaho[8]	129	~82	1	~12	2	•	5	12	9	•
Southeastern Manitoba[9]	107	18.6	1.9	15.9	58.9	0	17.8	0	0	•
South-central Alaska[10]	467	88.2	1.7	7.2	1.1	20.5	9.7	20.5	<1	1.3
Colorado[11]	47	~80	~42	~10	~6	~7	~9	•	~15	•
Vancouver Island[12]	701	~18	2	6	0	20	30	<1	<2	•

[1] *Soutiere (1979), 67% of material from April-September.*
[2] *More (1978), material from all seasons.*
[3] *Zielinski et al. (1983), material from all seasons.*
[4] *Douglas et al. (1983), scats from March-April and October-November over two-year period.*
[5] *Weckwerth and Hawley (1962), scats from all seasons over a five-year period.*
[6] *Cowan and Mackay (1950), season unknown.*
[7] *Lensink et a1. (1955), 80% of material from June-August.*
[8] *Koehler and Hornocker (1977), 63% of material from winter.*
[9] *Raine (1981), all winter scats.*
[10] *Buskirk and MacDonald (1984), scats from autumn, winter, and spring.*
[11] *Gordon (1986), all from winter.*
[12] *Nagorsen et al. (1989), all GI tracts from winter.*
▪ *Not mentioned, or cannot be inferred from data given.*

ing sites by sight and smell. In winter they forage on the snow surface, with forays up trees or into the subnivean space (Raine 1981; Spencer and Zielinski 1983; Zielinski et al. 1983). In the western United States in winter, most prey are captured beneath the snow surface, but squirrels may be caught in trees. In these areas, structure near the ground is important in providing access to subnivean spaces (Corn and Raphael 1992). In the eastern Canadian provinces, snowshoe hares are an important food and are caught on the snow surface or in slight depressions (Bateman 1986; Thompson and Colgan 1987).

Seasonal, Supra-annual, Geographic Variation in Diets

All data on diets of martens are disaggregated by study area (table 3), with some additional disaggregation by year, season, sex, and individual. Yearly variation is common and reflects the dynamics of food sources, especially prey numbers (Martin 1994; Thompson and Colgan 1987) and berry crops (Buskirk 1983).

Seasonal variation in marten diets is universal. Diets in summer include a wide range of food types, including mammals, birds and their eggs, fish, insects, and carrion. The importance of soft mast, especially the berries of *Vaccinium* and *Rubus,* peaks in autumn and declines over winter. As snow covers the ground and deepens, martens turn to mostly mammalian prey, which dominate the winter diet. The most important genera at this time are *Clethrionomys, Microtus, Spermophilus, Tamiasciurus*, and *Lepus*. There is a trend in some areas to turn to sciurids, especially *Tamiasciurus* sp. and *Spermophilus lateralis,* in late winter and early spring (Buskirk and MacDonald 1984; Zielinski et al. 1983). These seasonal patterns are largely explainable by food availability. Many of the birds and bird eggs (Gordon 1986) and fish (Nagorsen et al. 1989) eaten in summer are migratory and only seasonally present in marten home ranges. Insects that are active in summer burrow into soil or organic debris in winter. Fruits ripen in late summer but fall off plants or are covered with snow by early winter. And small mammals undergo wide seasonal changes in numbers and in physical accessibility (Buskirk and MacDonald 1984; Raine 1981; Zielinski et al. 1983). Mice and voles, which are captured beneath the snow, may decrease in their dietary importance as snow depths increase in late winter, and species that can be caught more easily, especially pine squirrels (*Tamiasciurus* spp.) and hares, increase in importance correspondingly (Martin 1994; Zielinski et al. 1983).

Geographic patterns reveal striking differences as well as some similarities. For example, snowshoe hares have been consistently more important prey in central and eastern Canada than farther west. But, although prey species vary across study areas, the same prey choices are not available everywhere. Martens often prey similarly on ecological analogues (e.g., *Tamiasciurus hudsonicus* and *T. douglasii*) in different areas, often under similar circumstances (c.f. Zielinski et al. 1983 with Buskirk: and MacDonald 1984). Martin (1994) showed that dietary diversity (Shannon-Weaver H') was lowest for high geographic latitudes (Buskirk and MacDonald 1984; Douglas et al. 1983; Lensink et al. 1955) and sites where martens eat mostly large-bodied prey, especially snowshoe hares (Bateman 1986; Raine 1987). The most diverse marten diets tended to be those from the west temperate part of the geographic range, including California.

Principal Prey Species

The most common prey species taken include red-backed voles (*Clethrionomys* spp.), voles (*Microtus montanus, M. oeconomus, M. pennsylvanicus, M. xanthognathus* and *Phenacomys intermedius*), pine squirrels (*Tamiasciurus* spp.), and ground squirrels (*Spermophilus* spp.). Of these, red-backed voles are staple, but not preferred, foods in most areas, being taken only in proportion to their availability (Buskirk and MacDonald 1984; Weckwerth and Hawley 1962). *Microtus* spp. are taken in excess of their availability in most areas. Martens capture them in small herbaceous or shrub patches (Buskirk. and MacDonald 1984), which in many areas are riparian (Zielinski et al. 1983). Deer mice and shrews are generally eaten less than expected based on their numerical abundance, but deer mice are the staple food on Vancouver Island, where red-backed voles are absent.

Martens appear to have important ecological relationships with red squirrels and Douglas squirrels. The active middens of these species provide resting sites that may be energetically important to martens in winter (Buskirk 1984, Spencer 1987). Middens also provide natal and maternal den sites (Ruggiero, in review). Sherburne and Bissonette (1993) found that martens gained access to the subnivean space via openings that were closer to squirrel middens than were openings not used by martens for subnivean access. The amount of coarse woody debris around access holes used and not used by martens did not differ. Although martens rest in active middens in some areas in winter, red and Douglas squirrels appear to have limited importance in the winter diet of martens in those locations (e.g., Alaska [Buskirk 1983]; Wyoming [Clark and Stromberg 1987]). This indicates that the two species may coexist at resting sites, and it further indicates that an important symbiosis may exist. This relationship may have important implications relative to marten habitat quality and to marten behaviors at times of energetic stress (Buskirk 1984).

Habitat Associations of Principal Prey

Red-backed voles are occupants of coniferous forests (Clough 1987; Nordyke and Buskirk 1991; Tevis 1956), where they associate closely with large-diameter logs (Hayes and Cross 1987) and understory plant cover (Nordyke and Buskirk 1991). Raphael (1989) showed that in the central Rocky Mountains, southern red-backed voles were most abundant in mature, mesic coniferous stands. The attributes with which red-backed voles associated most closely were high basal areas of Engelmann spruce and high old-growth scores. The old-growth attributes that contributed to a high score were multiple tree species contributing to the canopy, dense canopy, large-diameter trees, dense and large-diameter snags, and dense and large-diameter logs. *Microtus pennsylvanicus, M. montanus, M. oeconomus,* and *M. longicaudus* occupy herbaceous and shrub meadows. Red and Douglas squirrels are mostly restricted to coniferous forests of cone-producing stages, especially late-successional stages (Flyger and Gates 1982), although they can occur in hardwood stands in the eastern conterminous United States (Odum 1949). Snowshoe hares occur in a wide range of habitats (Bittner and Rongstad 1982) but generally prefer dense coniferous forests, dense early seral shrubs, and swamps interspersed with shrubs or saplings (Bookhout 1965; Richmond and Chien 1976). Dolbeer and Clark (1975) found that snowshoe hares in the central Rocky Mountains preferred mixed stands of spruce, subalpine fir, and lodgepole pine. Taiga voles, important foods of martens in taiga areas of Alaska and the Yukon, are variously reported to have wide habitat tolerances (Dougass 1977), be restricted to early post-fire seres (West 1979), or be associated with lightly burned forest (Wolff and Lidicker 1980).

Management Considerations

1. The most important prey of martens in the West in winter are forest species (*Clethrionomys* spp. and *Tamiasciurus* spp.) and herbaceous meadow or riparian species (*Microtus pennsylvanicus, M. montanus, M. xanthognathus,* others). Martens avoid deer mice in the sense of having a lower proportion of them in their scats than the proportion of deer mice among small mammals in the area. The same is; true for shrews. In the western United States in winter, the distribution and abundance of these species provide some measure of the value of habitats for foraging.

2. Abundance and availability of small mammals in winter are important determinants of fitness in martens. Habitats that provide an abundance of red-backed voles, pine squirrels (*Tamiasciurus* spp.), and meadow voles generally provide good foraging areas. Habitats with high densities of deer mice generally provide little in the way of foraging habitat.

3. Although major disturbance, including disturbance such as timber harvest activities, tends to increase populations of some small mammal species, especially deer mice, these species are not important prey for martens.

Research Needs

1. Document to what extent foraging habitat associations of martens are mediated by prey abundances as opposed to prey vulnerability. The latter may be affected by prey behavior, physical structure of habitat, and other factors.

2. Elucidate the relationship between pine squirrels (*Tamiasciurus* spp.) and martens with special emphasis on squirrels as prey and as builders of middens that are important resting sites and dens for martens. Whether middens are preferable to or an alternative for other structures as resting sites and natal and denning sites needs to be clarified.

HABITAT RELATIONSHIPS

General Considerations

Habitat quality is defined in terms of the fitness of animal occupants (Fretwell 1972). In the case of martens, fitness or components thereof are difficult to estimate, even by mammalian standards. Therefore, other attributes commonly are used as indicators of habitat quality, and we, like many who have studied marten habitats, accept the validity of this substitution although it is largely untested (Buskirk and Powell 1994; Ruggiero et al. 1988). The two most common attributes from which habitat quality is inferred in research studies are the behavioral choices of individual martens and population density, including some measure of population structure where possible.

The use of behavioral choices to indicate habitat quality assumes that martens recognize and prefer the best of a range of available habitats at some spatial scale (Ruggiero et al. 1988). It also requires that research be designed at spatial and temporal scales that will detect the important preferences of martens. Group selection has not been reported for any members of the genus *Martes;* therefore, using individual choices to reflect total fitness appears appropriate for this species (Buskirk and Powell 1994). The use of population density to indicate habitat quality involves assumptions discussed by Van Horne (1983). However, the marten appears to meet the criteria proposed by Van Horne for species in which population density is coupled to habitat quality. It is a habitat specialist, its reproductive rate is low, and it lacks patterns of social dominance in stable populations in high quality habitats, although there is evidence of avoidance by juveniles of high-quality habitats occupied by adults. Similarly, martens do not undergo seasonal shifts in home ranges, and only rarely do they migrate in the face of environmental unpredictability. Therefore, the use of population density to indicate habitat quality in the American marten should be valid, but this assumption has not specifically been tested.

Use of Major Vegetation Zones

Interpretations of studies of habitat use require that the context, sampling approach, and landscape of the study be understood. For example, stands in the Rocky Mountains dominated by lodgepole pine (*Pinus contorta*) are variously described as preferred (Fager 1991), used in proportion to availability (Buskirk et al. 1989), or avoided (Wilbert 1992) based on the spatial extent of lodgepole types. But this apparent discrepancy is largely due to variation in landscapes studied, rather than habitat plasticity of martens. If a study area contains roughly even proportions of a highly preferred mesic forest type, a dry, less preferred forest type, and nonforested habitat, the lodgepole pine is more likely to be used in proportion to availability than if the nonforested habitat is not considered in the study or not present in the study area. Also, rejection of null hypotheses regarding habitat selection depends on the power in the statistical tests. Studies involving small numbers of animals or other units of replication are likely to conclude that martens are habitat generalists.

Broadly, American martens are limited to conifer-dominated forests and vegetation types nearby. In most studies of habitat use, martens were found to prefer late-successional stands of mesic coniferous forest, especially those with complex physical structure near the ground (Buskirk and Powell 1994). Xeric forest types and those with a lack of structure near the ground are used little or not at all. In the northern part of its range, xeric coniferous stands are not available to the American marten; therefore, this site moisture preference is not seen here, but the preference and apparent need for structure near the ground, especially in winter, appears universal.

Complex physical structure, especially near the ground, appears to address three important life needs of martens. It provides protection from predators, it provides access to the subnivean space where most prey are captured in winter, and it provides protective thermal microenvironments, especially in winter (Buskirk and Powell 1994). Structure near the ground may be contributed in various ways, including coarse woody debris recruited by gradual tree death and tree fall (Buskirk et al. 1989), coarse woody debris recruited en masse by fire (Harmon et al. 1986), the lower branches of living trees (Buskirk et al. 1989), rock fields in forests (Buskirk et al. 1989), talus fields above treeline (Streeter and Braun 1968), shrubs (Hargis and McCullough 1984), herbaceous plants (Spencer et al. 1983), squirrel middens (Finley 1969), and combinations of these.

Preferences for major vegetation types vary across geographic areas and have been reviewed by Bennett and Samson (1984). This variation may seem to contradict the habitat specialization of the species, but closer examination shows that the requirement for structure near the ground is constant and that the same tree species show different site and structural attributes across regions. On the west slope of the Cascade Range, Jones and Raphael (1991, unpubl. data) reported that old-growth forests within the Pacific silver fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) zones were preferred by 14 martens, based on 1,292 telemetry locations. Clearcuts were used less than expected from their availability, and the largest diameter trees available typically were used as resting sites. In Okanogan County, Washington, Koehler et al. (1990) found 10 of 11 marten tracks in stands dominated by Engelmann spruce (*Picea engelmannii*) --- subalpine fir (*Abies lasiocarpa*) and lodgepole pine >82 years old. These two types represented 51 % of the area sampled. Marten tracks were rare or absent in stands dominated by younger lodgepole pine and Douglas fir (*Pseudotsuga menziesii*), larch, and aspen. On Vancouver Island, Baker (1992) found martens in 10- to 40-year-old second-growth Douglas fir more than in old-growth western hemlock-Pacific silver fir-western redcedar (*Thuja plicata*). However, structures used by martens for resting generally were residual components of the pre-existing old-growth stands. In the Sierra Nevadas, martens were shown to prefer lodgepole pine in riparian settings and red fir at higher elevations and to avoid Jeffrey pine (*Pinus jeffreyi*) associations (Simon 1980; Spencer et al. 1983). In interior Alaska martens occupy both of the major forest types available, dominated by white spruce (*Picea glauca*) and black spruce (*P. mariana*) (Buskirk 1983). In Ontario, martens preferred stands with some conifer component over pure hardwood stands (Francis and Stephenson 1972; Taylor and Abrey 1982). Snyder and Bissonette (1987) found that martens on Newfoundland Island occurred in stands dominated by balsam fir (*Abies balsamea*) and black spruce. In various sites in the northern Rocky Mountains, martens have preferred stands dominated by mesic subalpine fir, Douglas fir, and lodgepole pine in some associations, and martens have used stands dominated by xeric subalpine fir and lodgepole pine in other associations less than predicted from the spatial availability of these types (Burnett 1981; Fager 1991). In the central and southern Rockies, martens prefer stands dominated by spruce (*Picea* spp.) and subalpine fir, occur in stands dominated by lodgepole pine and limber pine (*P. flexilis*), and are rare or absent in stands dominated by ponderosa pine or pinyon pine (*P. edulis*) (Buskirk et al. 1989; Wilbert 1992). In no place have American martens been found to prefer hardwood-dominated stands over conifer-dominated stands.

Use or selection of riparian zones has been reported by several authors. Buskirk et al. (1989) reported preference for riparian areas for resting, and Spencer and Zielinski (1983) reported foraging in riparian areas. Jones and Raphael (1992, unpubl. data) also reported heavy use of areas close to streams.

Habitat Use in Relation to Sex, Age, and Season

The selection of natal den habitat by females likely is an example of a gender-specific habitat selection, but it is unclear whether females select den sites that differ from male resting sites. Descriptions of natal dens are scarce. In all cases involving trees, large structures associated with late-seral forest conditions were used, and in Wyoming, martens selected for old-growth characteristics at 14 natal dens (Ruggiero, in review). Baker (1992) showed that female martens were more selective of habitats than were males and hypothesized that this difference was due to more stringent demands for resources placed on females by reproduction.

Age-specific habitat associations have been reported in some studies that looked for them. For example, Burnett (1981) concluded that juveniles occupied a wider range of habitat types than did adults. Likewise, Buskirk et al. (1989) showed that although martens ≥1 year old preferred spruce-fir stands for resting, juveniles were not selective of any stand type. Spruce-fir stands had higher basal areas, larger-diameter trees, and higher densities and diameters of logs than did lodgepole stands, and resting sites were presumed to be more common in the former. Juveniles may fail to recognize, or may be excluded by territorial adults of the same sex, from high-quality habitats (Buskirk et al. 1989). Therefore, habitat choices by juveniles may be constrained by the behaviors of dominant adults, with important implications for juvenile survival. For example, Baker (1992) reported that two juveniles using early successional habitats in a logged landscape were killed by great-horned owls (*Bubo virginianus*). Juveniles may maximize their fitness by choosing from among a set of habitats that exclude the best habitats occupied by conspecifics in the area. This age-dependent habitat selection has important implications for our understanding of the habitat needs of martens, and possibly for the density - habitat quality relationship. If juveniles are less habitat-selective (or more habitat constrained) than adults, which they appear to be, and because juveniles are more likely to be captured, and therefore radio-collared and studied, habitat studies that do not specifically consider the effect of age on habitat selection may characterize martens as far less habitat-specialized than they are as reproducing adults. For this reason, it is vitally important in studies of habitat preference to focus on the fitness of individuals, and persistence of populations, rather than on the mere presence of individuals in particular habitats for brief periods (Ruggiero et al. 1988).

Seasonal variation in habitat selection has been reported by most authors who have analyzed their data for it. There is little evidence of shifts of home range boundaries to seasonally encompass different habitat types; therefore, martens seasonally adjust their selection of stands within stable home ranges. Campbell (1979), Soutiere (1979), Steventon and Major (1982), and Wilbert (1992) all reported more selective use of late- successional coniferous stands in winter than in summer. Koehler and Hornocker (1977) reported more selective use of habitats in deep snow than in shallow snow. Buskirk et al. (1989) showed that in winter marten were more likely to use spruce-fir with more old-growth character in cold weather than in warm weather. No studies have shown the converse pattern. Of the studies that have compared summer and winter use of nonforested habitats, all report less use in winter (Koehler and Hornocker 1977; Soutiere 1979) and in some cases no use (Spencer et al. 1983). The possible reasons for this seasonal variation have been reviewed by Buskirk and Powell (1994) and include the greater visibility of martens to potential predators on a snow background, and the greater importance of structure near the ground in providing foraging sites in winter. This seasonal variation also has important implications for understanding the results of habitat studies. Habitat studies conducted during winter are more likely than those in summer to conclude that martens strongly prefer late-successional conifers. Winter, therefore, appears to be the season when martens in most areas are limited to the narrowest range of habitats within their home ranges.

Special Requirements and Spatial Scales

Microhabitat Use

The smallest scale at which habitat use has been investigated involves use of resting sites (e.g., Buskirk et al. 1989; Taylor 1993; Wilbert 1992), natal and maternal dens (Henry and Ruggiero, in press; Ruggiero, in review), and access sites to spaces beneath the snow (Corn and Raphael 1992; Sherburne and Bissonette 1993). Wilbert (1992) found that martens selected boles for resting that were larger than those in surrounding plots, and logs that were in intermediate stages of decomposition. Taylor (1993) showed that martens could reduce thermoregulatory costs by selecting from among the resting site types available over small areas. Wilbert (1992) also found that structural variability was itself selected for resting. Natal dens were in the largest boles available in Ruggiero's (in review) study area. Corn and Raphael (1992) showed that martens gained access to subnivean spaces via openings created by coarse woody debris at low snow depths, and by lower branches of live trees in deep snow. Compared with marten trails generally, subnivean access points had higher volumes of coarse woody debris, more log layers, and fewer logs in advanced states of decay. These findings support the view that marten. are highly selective of microenvironments for thermal cover, for protection from predators, and for access to subnivean foraging sites.

Landscape-Scale Habitat Use

Knowledge is almost completely lacking regarding behavioral or population responses of martens to such landscape attributes as stand size, stand shape, area of stand interiors, amount of edge, stand insularity, use of corridors, and connectivity (Buskirk 1992). Snyder and Bissonette (1987) reported that marten use of residual forest stands surrounded by clearcuts on Newfoundland Island was a function of stand size. Stands <15 ha in area had lower capture success rates than larger stands. However, the dearth of knowledge in this area makes managing forested landscapes for martens highly conjectural.

Effects of Forest Fragmentation

Fragmentation includes loss of stand area, loss of stand interior area, changes in relative or absolute amounts of stand edge, and changes in insularity (Turner 1989). The term is context-specific but is more commonly used to characterize major retrogressional changes to late-successional forests than successional processes affecting early seres. Again, marten responses to these processes above the stand level are completely unstudied; virtually no knowledge exists that would allow scientific management of fragmentation processes to accommodate martens. Brainerd (1990) presented a general hypothesis of the response of Eurasian pine martens (*Martes martes*) to forest fragmentation, which predicted that marten populations would increase in response to forest fragmentation that cut small patches and left 45% of pristine forest intact. The reasoning behind this prediction is that *Microtus* are abundant in Scandinavian clearcuts, and if these cuts are small enough that martens can forage in them and remain close to trees, then a positive numerical response should result. Brainerd (1990) also predicted that cutting of larger patches should reduce marten densities. Brainerd's model may be relevant to North America; however, the lack of any *Microtus* or other preferred prey species that responds positively to clearcutting of conifers in the western conterminous United States limits the applicability of this model.

Response to Human Disturbances

The effect of major retrogressional change on stand-level habitat selection has been studied in several areas (Bateman 1986; Francis and Stephenson 1972; Soutiere 1979; Spencer et al. 1983; Thompson 1994). Among the habitat types included in these studies have been clearcuts and selective ("partial") cuts in various stages of regeneration. These studies have generally shown that martens make little absolute or relative use of clearcuts for several decades and that marten populations decline after clearcut logging. Soutiere (1979) showed that marten densities in clearcut areas in Maine were 0.4/km^2, about one-third of those in uncut and partially cut stands. In partially cut stands all balsam fir (*Abies balsamae*) 15 cm or greater dbh, and all spruce and hardwoods 40 cm or greater dbh had been removed so that, among stands, 57-84% of basal area had been removed. Soutiere (1979:850) believed that retention of 20-25 m^2/ha basal area of trees in pole and larger trees "provided adequate habitat for marten." The clearcut logging had taken place 1-15 years before the study. But Steventon and Major (1982) found that use of clearcuts in the same study area was limited to summer. Self and Kerns (1992, unpubl.) studied habitat use by three martens in northcentral California and suggested that martens did not show strong habitat selection. However, they did not report any statistical analyses of habitat use upon which inferences were based. Thompson and Harestad (1994) summarized the results of 10 studies of habitat selection in relation to successional stage. These studies showed consistent use/ availability ratios <1 in shrub, sapling, and pole stages. Only when successsion reached the "mature" stage did use/availability ratios begin to exceed one, and only "overmature" stands were consistently preferred. None of the studies found use/availability ratios for "overmature" stands <1 (Thompson and Harestad 1994). Baker

(1992) described the most striking exception to this pattern from Vancouver Island. She found preference for 10- to 40-year-old post-cutting Douglas fir over old-growth types. However, her study area was unusual in that large-diameter coarse woody debris predating the cutting provided structures not ordinarily found in second-growth stands. Almost no other studies specific to western North America show how marten preference for regenerating clearcut stands varies with time.

For North America generally, Thompson and Harestad (1994) reviewed literature on the duration of the negative effects of clearcut logging on martens. They concluded that for the first 45 years post-cutting, regenerating clearcuts supported 0-33% of the marten population levels found in nearby uncut forest, and by inference, in the pre-cut forest. Thompson (1994) reported that some martens occupied areas that had been clearcut 10-40 years before but that these animals experienced high mortality rates from predation and trapping.

The mechanisms by which martens are impacted by timber cutting are the removal of overhead cover, the removal of large-diameter coarse woody debris, and, in the case of clearcutting, the conversion of mesic sites to xeric sites, with associated changes in prey communities (Campbell 1979). Some of these effects, such as loss of canopy cover, can be reversed by succession in the near-term. Others, including the removal of coarse woody debris, can only be reversed by the addition of coarse woody debris or by the growth of new large-diameter boles.

Structural Features Relative to Succession

The structural features that develop with successional advancement and that are important to martens include overhead cover, especially near the ground; high volumes of coarse woody debris, especially of large diameter; and small-scale horizontal heterogeneity of vegetation, including the interspersion of herbaceous patches with patches of large, old trees. Overhead cover is important because it confers protection from predators and addresses the behavioral preference of martens for areas with cover (Hawley and Newby 1957). Some early successional stages provide overhead cover in the form of dense herbaceous or shrubby vegetation (Magoun and Vernam 1986). In later successional stages, this need is met by the lower branches of living trees, by coarse woody debris, and by squirrel middens. One important change that occurs with succession is the replacement of shade-intolerant tree species with shade-tolerant ones. The latter (e.g., spruce and fir) retain lower branches on the bole in shaded settings, contributing to structure near the ground in forests with dense canopy (Peet 1988). However, the behavioral avoidance of openings by martens shows geographic variation, with martens in taiga areas of Alaska and the Yukon apparently showing greater tolerance of sparse canopy than martens farther south (Buskirk 1983; Magoun and Vernam 1986).

Some kinds of major retrogressional change also produce structural conditions preferred by martens. Considerable work in Alaska shows that martens attain high local densities in post-fire seres that have complex physical structure in the form of horizontal boles or dense herbaceous vegetation (Johnson and Paragi 1993; Magoun and Vernam 1986). However, Fager (1991) found almost no use of forests burned by the 1988 Yellowstone fires, although martens passed through burns and rested in unburned islands. Therefore, marten responses to burns appear to vary regionally, but it is not clear whether behaviors of martens or site responses to fire produce this variation.

Horizontal heterogeneity may be important because it allows martens to fulfill their life needs in small areas, reducing travel distances. Martens may be especially benefitted by the small-scale horizontal heterogeneity that results from the natural dynamics of old-growth forests (Hunter 1990). For example, the death of large old trees results in tree boles falling to the forest floor. In this position, they are important for overhead cover and for natal dens and maternal dens, and for winter resting sites. At the same time, opening of the canopy by the loss of large old trees admits sunlight to the forest floor, which stimulates herbaceous growth, which may in turn attract or produce small pockets of mice or voles (Hunter 1990), important prey for martens. It is not clear whether selective harvest of trees could mimic these small disturbances.

Coarse woody debris, especially in the form of large-diameter tree boles, can address many of the needs that martens have for physical structure: predator avoidance, access to subnivean spaces (Corn and Raphael 1992), and thermal protection (Buskirk et al. 1989). Coarse woody debris accumulates in volume with advancing succession, and logs in old mesic coniferous stands are larger in diameter than those in young ones (Harmon et al. 1986). Also, in unmanaged forests, coarse woody debris accumulates more and attains higher diameters in mesic stands that have not been disturbed by fire than in xeric stands that have. Of course, human changes to the dynamics of coarse woody debris alter these relationships.

The processes of tree death and decay alter the position, shape, internal structure, and physical properties of boles (Harmon et al. 1986) to make them more important features of marten habitats. Pathogen-induced changes in the growth form of conifers can create important microenvironments ("witch's brooms") for martens (Buskirk et al. 1989). Wind fells rot-weakened boles of old trees to positions near the ground, and the hollows created by decay in logs and stumps are used by martens for resting sites and natal dens (see Buskirk et al. [1987] for review). Partially decayed wood may have physical properties that affect the microenvironments used by martens. Lastly, other vertebrate occupants of late-successional forests cause structural changes that are important to martens. These include primary cavity-nesting birds, which build cavities in boles, and red and Douglas squirrels, which build leaf nests in trees and underground nests in piles of conifer cone bracts (Finley 1969). All of these structures are important to martens for resting (Buskirk 1984; Spencer 1987; Wilbert 1992).

Use of Nonforested Habitats

Martens generally avoid habitats that lack overhead cover. These habitats include prairies, herbaceous parklands or meadows, clearcuts, and tundra. In an evaluation of placement of bait stations to avoid nontarget effects, Robinson (1953) found that martens avoided traveling >23 m from forest edges in Colorado. Fager (1991), Koehler and Hornocker (1977), Soutiere (1979), Simon (1980), and Spencer et al. (1983) have reported complete or partial avoidance of nonforested habitats. The size of openings that martens have been observed to cross have varied from 10 m (Spencer et al. 1983) to 40 m (Simon 1980) to 100 m (Koehler and Hornocker 1977). In most cases, these are the largest openings that the authors observed to be crossed during their respective studies. Buskirk (1983) described a marten crossing a 300-m wide unforested river bar in winter during a home-range shift. Soutiere (1979) reported martens crossing clearcuts in winter and stopping to investigate woody debris protruding from the snow. Hargis and McCullough (1984) reported martens crossing meadows but not stopping to rest or forage. However, summer use of nonforested habitats above treeline is common in the montane part of the distribution. Streeter and Braun (1968) documented martens in talus fields 0.8-3.2 km from the nearest forest in Colorado, and Grinnell et al. (1937) reported similar use of talus fields in the Sierra Nevadas in summer. Also, martens forage in some herbaceous and low-shrub meadow openings if suitable prey, especially Microtus, are available (Buskirk and Powell 1994; Martin 1994).

The Refugium Concept

For over 40 years, researchers have emphasized the importance of refugia to the conservation of American martens. DeVos (1951) first pointed out that the difficult and inferential nature of population monitoring for martens required landscape designs that assured population persistence. The refugium concept has been advocated often since then (Archibald and Jessup 1984; Strickland 1994; Thompson and Colgan 1987), and the broad outlines of such a conservation design have been stated (Howe et al. 1991). Clearly, the refugium concept is a nonquantitative application to wildlife management of the principles embodied in source-sink theory (Pulliam 1988). However, many specific features of refugium systems that would assure population persistence of martens have not been stated or involve untested assumptions (Buskirk, in press). These include habitat quality of refugia relative to areas where martens are trapped or timber is cut, and sizes of and permissible distances separating refugia. To implement a system of refugia for conserving American martens, the parameters of such a system must be derived and tested.

Management Considerations

1. Although American martens at times use other habitats, populations depend on (*sensu* Ruggiero et al. 1988) coniferous forests. Martens associate closely with mesic, late-successional coniferous forests but occur in other vegetation types. They use treeless areas less than predicted from their spatial availability, especially in winter. Clearcutting reduces marten densities for several decades. In some areas, under conditions that are not well understood, martens may use regenerating clearcuts after a decade or two if sufficient structures useful to martens persist from

the clearcutting. The effect of other cutting regimes, including small patch cutting, seed tree cutting, or salvage harvest of dead or damaged timber have not been widely studied.

2. Coarse woody debris, especially in the form of large-diameter boles, is an important feature of marten habitat. Logs are most useful to martens for gaining access to subnivean areas and for resting. Removal of coarse woody debris from forests or interfering with processes that make it available in suitable sizes and stages of decay may reduce habitat quality for martens.

Research Needs

1. To design conservation strategies at stand and landscape scales, we need better understanding of how martens use edges and small, nonforested openings. These features are too small to be studied by traditional research techniques. Examples of small nonforested openings include patch cuts, small herbaceous meadows, and breaks in the canopy caused by deaths of individual trees. Pursuing this goal will require gathering data that have measurement error that is small relative to the size of the feature that is being studied.

2. Determine habitat quality gradients affecting the density and fitness of marten populations. There is also a need to test the assumption that the habitats that have the highest marten densities confer the highest fitness on occupants. This information is important for understanding the differences between habitat occupancy and habitat quality.

3. Obtain better knowledge of how landscape attributes, including stand size, stand shape, area of stand interiors, amount of edge, stand insularity, corridors, and connectivity affect marten populations.

4. To provide cost-effective means of assessing habitat quality for martens, perform a systematic evaluation of existing models of marten habitat quality (e.g., Allen 1984), such as has been done for fishers (Thomasma et al. 1991).

5. In order to understand the meaning of past studies that have examined habitat preferences, investigate how sex, age, and social rank affect habitat choices.

6. To place the habitat use of martens into the context of source-sink theory, determine how habitat quality gradients affect juvenile survival rates, dispersal rates, directions, and distances. This has important implications for understanding population insularity and metapopulation structure.

HOME RANGE

Variation in Home Range Attributes

Home ranges of American martens, usually in the sense used by Burt (1943), have been described for many study sites, and home range size has been reported in over 26 published accounts (Buskirk and McDonald 1989). Home range data usually consist of two-dimensional sizes, with additional information on shape, use intensity within the home range, and spatial relationships among home ranges. Buskirk and McDonald (1989) analyzed patterns of variation in home-range sizes from nine study sites and found that most variation was unexplained. among-site variation. Male home ranges varied significantly among sites, but those of females did not. The largest home ranges, described by Mech and Rogers (1977) from Minnesota (male mean = 15.7 km^2), were about 25 times the size of the smallest ones (male mean = 0.8 km^2) reported by Burnett (1981) from Montana. Home range size was not correlated with latitude or with an index of seasonality Male home range sizes were 1.9 times those of females, but no significant age variation was observed.

Marten home ranges are large by mammalian standards. Harestad and Bunnell (1979) and Lindstedt et al. (1986) developed allometric equations for home range size for mammalian carnivores and herbivores. Averaging all study site means reviewed by Buskirk and McDonald (1989), home ranges of American martens are 3-4 times larger than predicted for a 1-kg terrestrial carnivoren, and about 30 times that predicted for an herbivorous mammal of that size.

In addition to sex and geographic area, home range size of martens has been shown to vary as a function of prey abundance (Thompson and Colgan 1987) and habitat type (Soutiere 1979; Thompson and Colgan 1987). Soutiere (1979) found home range sizes about 63% larger in clearcut forest than in selectively cut and uncut forest in Maine. Thompson and Colgan (1987) reported even more striking differences from Ontario, with home ranges in clearcut areas 1.5-3.1 times the size of those in uncut areas.

Territoriality

Intrasexual territory of most or all of the adult home range has been generally inferred, as it has for other *Martes* species (Powell 1994). This inference is based on the greater overlap of home ranges between than within sexes (Baker 1992; Francis and Stephenson 1972; Hawley and Newby 1957; Simon 1980), on observations of intrasexual strife (Raine 1981; Strickland and Douglas 1987), and on the pattern exhibited by other solitary Mustelidae (Powell 1979). Juveniles and transients of both sexes apparently occupy neither territories nor true home ranges (Strickland and Douglas 1987).

Spatial Relationships Among Cohorts

Martens exhibit the pattern of spatial organization that is typical of solitary Carnivora: intrasexual territoriality among residents (Ewer 1973; Powell 1979). In addition, geographically and temporally variable numbers of transients, as well as predispersal young, occur in the home ranges of adults of both sexes. Because male home ranges are larger, they must be the space-limited cohort under conditions of equal sex ratio.

Management Considerations

1. Marten home ranges are very large, a correlate of low population densities. Martens must assemble home ranges from landscapes, rather than stands.

Research Needs

1. We need better knowledge of the relationship between home range size and specific habitat attributes, such as forested area in specific successional or structural stages. To manage forested landscapes for martens, we need better knowledge of how home range size varies as a function of landscape attributes, such as those involving forest interior, edge, and stand connectivity.
2. To relate habitat quality to fitness, we need better knowledge of the amounts of particular habitat types, especially late-successional forest, that must be incorporated into a marten home range in order for a marten to survive and for a female to produce litters.
3. There is a need for more rigorous methods of inferring population density from home range data. We need to identify the assumptions underlying the conversion of home range size to population density. We also need better understanding of the relationship between habitat attributes and the degree to which habitat is saturated with home ranges.

MOVEMENTS

Movements of martens beyond home range boundaries, including dispersal and migration, have been studied little. This is a result of the technical difficulty and high cost of studying long-distance movements in small-bodied mammals. Reports of long-distance movements, likely representing dispersal, are largely anecdotal. Archibald and Jessup (1984) reported two periods of dispersal, one from about mid-July to mid-September, and the other over winter. They inferred the onset of dispersal by the arrival of new nonresident animals, mostly juveniles, in their study area. However, the timing of dispersal has not been consistent among studies and ranges from early August to October (Slough 1989). Clark and Campbell (1976) reported a period of shifting during late winter and spring. For most of the year, marten populations may include some animals without true home ranges.

Migration by martens, involving unidirectional movements by many animals, have been reported by trappers in Alaska (Buskirk 1983:44) and elsewhere but have not been documented in the scientific literature.

Management Considerations

1. The long dispersal distances of martens, to the extent that we understand them, in combination with the sensitivity of martens to overhead cover suggest that connectivity of habitat providing overhead cover is important to population dynamics and colonization.

Research Needs

1. Investigate the relationship between habitat and dispersal attributes if we are to understand natural colonization of habitats and metapopulation structure.

COMMUNITY INTERACTIONS

DeVos (1952) reported killing of martens by fishers, and Raine (1981) found marten remains in fisher scats but acknowledged that the remains could have represented scavenging. Various mammalian predators (Jones and Raphael 1991, unpubl.; Nelson 1973) and raptors and owls (Clark et al. 1987) have been reported to kill martens. Because martens scavenge carcasses of animals killed by other predators (see General Foraging Ecology and Behavior section), they may be considered to be commensal, at least at some times. Other important community interactions not involving predation include the use by martens of cavities built by birds for resting and denning, and of resting structures built by red and Douglas squirrels (see Habitat Relationships section). Squirrel middens appear to represent an important habitat need in some areas (Buskirk 1984; Ruggiero, in review; Sherburne and Bissonette 1993), but this relationship is poorly understood. The greater ability of martens than of fishers to travel across deep, soft snow (Raine 1981) may result in partitioning of habitats between martens and fishers along lines of snow attributes. American martens have been hypothesized to serve as important dispersal agents of the seeds of fleshy-fruited angiosperms (Willson 1992). This function is enhanced by the high frugivory (table 3) and wide-ranging behaviors of martens.

Management Considerations

1. The abundance of other mammalian predators may affect marten behaviors or populations.

2. The close association of martens and pine squirrels (*Tamiasciurus*) in many areas suggests that management actions that affect pine squirrel populations will affect marten populations.

Research Needs

1. Investigate how habitat-generalist predators may affect survival of martens, especially in managed forests.

2. Investigate the symbiotic relationship between martens and red and Douglas squirrels, including predator-prey relationships and use by martens of structures built or modified by squirrels.

CONSERVATION STATUS

1. In the western conterminous United States, the marten has undergone major reductions in distribution. These changes are poorly understood for some areas because of fragmentary or unreliable data. The geographic range has apparently been fragmented, especially in the Pacific Northwest. The reduction and fragmentation of the geographic range of martens has resulted primarily from the loss of habitat due to timber cutting. The only range expansions in the western United States are the result of transplants to islands in southeast Alaska.

2. In the Rocky Mountains and Sierra Nevadas, the marten has a geographic range apparently similar to that in presettlement historical times. Population levels are not known reliably enough to compare current population levels with those at any earlier time.

3. A named subspecies, *Martes americana humboldtensis,* may be threatened or endangered in northwestern California. The most likely cause of this hypothesized status is loss of habitat due to timber cutting.

4. Several marten populations are known or hypothesized to have been isolated by human-caused habitat change. The genetic and stochastic processes that predispose small populations to extinction likely are acting on these remnants.

5. The marten is predisposed by several attributes to impacts from human activities. These attributes include its habitat specialization for mesic, structurally complex forests; its low population densities; its low reproductive rate for a mammal of its size; and its vulnerability to trapping. Counteracting these factors, the marten is small-bodied and has more favorable life history traits, from a conservation standpoint, than some larger-bodied Carnivora.

6. The effects of trapping on marten populations over most of the western conterminous United States likely are local and transient. However, trapping may adversely affect some marten populations and may have contributed to or hastened local extinctions, especially where habitat quality was poor. Also, populations that are kept at artificially low levels by trapping should not be expected to respond to resource limitations, such as limited prey, except under conditions of extreme resource scarcity.

7. Clearcutting, the most common timber harvesting practice in the northwestern United States in the last 20 years, is generally deleterious to marten populations. Regenerating clearcuts have little or no value as marten habitat for several decades. However, this loss of habitat quality may not occur in all areas. Generally, consistent preference is not shown by martens until stands reach the "mature" or "overmature" stage.

8. Changes in patterns of distribution and abundance of martens indicate that this species is not secure throughout its range. In areas where populations appear to have been isolated by human actions, or where already isolated populations have had the carrying capacity of the habitat reduced, immediate measures to ensure persistence appear prudent. Given the marten's association with late-successional

forests, we believe there is an urgent need to base further assessments of conservation status on additional research addressing issues of marten-landscape relationships.

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