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The Scientific Basis for Conserving Forest Carnivores

American Marten, Fisher, Lynx, and Wolverine

in the Western United States

Abstract

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This cooperative effort by USDA Forest Service Research and the National Forest System assesses the state of knowledge related to the conservation status of four forest carnivores in the western United States: American marten, fisher, lynx, and wolverine. The conservation assessment reviews the biology and ecology of these species. It also discusses management considerations stemming from what is known and identifies information needed. Overall, we found huge knowledge gaps that make it difficult to evaluate the species' conservation status.

In the western United States, the forest carnivores in this assessment are limited to boreal forest ecosystems. These forests are characterized by extensive landscapes with a component of structurally complex, mesic coniferous stands that are characteristic of late stages of forest development. The center of the distrbution of this forest type, and of forest carnivores, is the vast boreal forest of Canada and Alaska. In the western conterminous 48 states, the distribution of boreal forest is less continuous and more isolated so that forest carnivores and their habitats are more fragmented at the southern limits of their ranges. Forest carnivores tend to be wilderness species, are largely intolerant of human activities, and tend to have low reproductive rates and large spatial requirements by mammalian standards.

We must have information at the stand and landscape scales if we are to develop reliable conservation strategies for forest carnivores. Ecosystem management appears likely to be central to these conservation strategies. Complex physical structure associated with mesic late successional forests will be important in forest carnivore conservation plans. Immediate conservation measures will be needed to conserve forest carnivore populations that are small and isolated. Additional forest fragmentation especially through clearcutting of contiguous forest may be detrimental to the conservation of forest carnivores, especially the fisher and marten. Specific effects will depend on the context within which management actions occur.

Keywords: American marten, fisher, lynx, wolverine, late-successional forest, old growth, conservation biology, fragmentation, wilderness, *Martes americana, Martes pennanti, Lynx canadensis, Gulo gulo*

Cover: Fisher, lynx, and wolverine photos by Susan C. Morse of Morse & Morse Forestry and Wildlife Consultants. Marten photo by Dan Hartrnan.

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American Marten, Fisher, Lynx, and Wolverine

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Preface

This book assesses the scientific basis for conserving the American marten, fisher, lynx, and wolverine. It consists of literature reviews for each species and a discussion of management considerations and information needs. The species' accounts were written by recognized authorities who were asked to review and synthesize existing knowledge about the biology and ecology of each species, paying particular attention to aspects of their natural histories that affect the conservation of populations in the western montane regions of the conterminous United States. In Chapter 6, we evaluate this knowledge base and discuss considerations for land managers. Chapter 7 describes what is critically needed to develop scientifically sound conservation strategies for each species. Throughout the text, we have used the term "unpublished" as an integral part of a citation when reference is made to a document that has not been peer reviewed and is not widely available as a printed document. We hope readers will find this helpful in evaluating the nature of a citation without constantly referring to the literature cited sections.

Our efforts and those of our collaborators build on the foundation of information that has been established by others. In addition to the researchers who produced the information summarized in this book, we acknowledge the important contributions of Bill Ruediger and John Weaver. Bill is responsible for organizing the Western Forest Carnivore Committee, a group dedicated to coordinating the activities and concerns of state and federal agencies and various nongovernmental organizations. In his role as Threatened, Endangered, and Sensitive Species Program Manager for the Northern Region of the National Forest System, Bill also sponsored the development of useful literature reviews on the fisher, lynx, and wolverine. Finally, Bill suggested to Jack Lyon a method by which Forest Service Research could synthesize existing information on the fisher, lynx, and wolverine and develop a research approach. The result was a contract with John Weaver, through the Intermountain Research Station, for a synthesis and recommendations for needed research. John's work stands out as an important contribution to our knowledge of forest carnivores. Both of these individuals have made significant contributions to the conservation of forest carnivores, and we are indebted to them for their efforts.

The material in Appendix C was developed through considerable effort by our management partners. Chris Jauhola and Diane Macfarlane of the Pacific Southwest Region of the National Forest System led the management portion of our conservation assessment team. We greatly appreciate their efforts. Special thanks to Erin O'Doherty of the Rocky Mountain Forest and Range Experiment Station for assistance in compiling the maps in Appendix B. We thank the British Columbia Ministry of Environment, Lands, and Parks, Wildlife Branch, especially Ray Halladay, for cooperation in producing the ecological stratification scheme presented in Appendix A. We also thank Tom Hoekstra and Mike Lennartz of Forest Service Research and Phil Janik and Dale Bosworth of the National Forest System for their guidance throughout the conservation assessment process.

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Chapter 1

A Conservation Assessment Framework for Forest Carnivores

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BACKGROUND

Controversy over managing public lands is neither an unexpected nor recent development. In the 1970's, debate over land management began to focus on the effects of timber management practices on wildlife. This was most evident in the Pacific Northwest where the public was beginning to express strong concerns about the effects of timber harvest in late-successional forests on northern spotted owls and other vertebrates. The focus on all vertebrates and not just "game animals" distinguished these concerns from earlier wildlife-related issues. In 1976, Congress passed the National Forest Management Act, which mandated the maintenance of biological diversity on lands of the National Forest System. Regulations enacted pursuant to this law specified that viable populations of native and desirable non-native wildlife species would be maintained on planning units (i.e., National Forests) of the National Forest System. Thus, a statutory and regulatory basis was provided for appeals and litigation directed at what the public believed to be the negative effects of timber management practices on wildlife. The many legal challenges that ensued focused primarily on the harvesting of late-successional forests in the Pacific Northwest (see Meslow et al. 1981 for additional discussion).

The USDA Forest Service responded to this situation in 1981 by chartering a research and development program aimed at studying the role of old-growth forests as wildlife habitat (Ruggiero et al. 1991). Early research efforts of this program focused on the ecology of spotted owls, a species at the center of the most intense debate. Although research was underway, legal challenges disrupted forest management activities, and the controversy was played out in legal and political arenas. Science was not called on as part of the solution until nearly a decade later, *after* the development of a political impasse in one of the country's most important timber-producing regions. In 1989, in response to this impasse, an interagency agreement between the major land management agencies established the "Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl." The charter of this group was later incorporated into law (Section 318 of Public Law 101-121), and a conservation strategy for the northern spotted resulted (Thomas et al. 1990). In 1991, Congress intervened directly by commissioning the Scientific Panel on Late-Successional Forest Ecosystems, whose mission was to make broad recommendations about management of the remaining old-growth forests in the Pacific Northwest (Johnson et al. 1991). And, in 1993, President Bill Clinton intervened and

appointed a task force of scientists to evaluate the effects of alternative management scenarios for old-growth forests on all wildlife in the Pacific Northwest (Thomas et al. 1993a). This intervention included an unprecedented visit by a U.S. president to the site of a regional forest management/ wildlife controversy for the purpose of facilitating its end (the Forest Conference convened in Portland, Oregon, on April 2, 1993).

It is clear from these events that public concern over the effects of land management on wildlife is enormously important politically, economically, and scientifically. It is also clear that the conservation strategy for the northern spotted owl came too late. Nearly two decades passed from the first concerns over the conservation status of this subspecies until scientists were asked to develop a "scientifically credible" conservation strategy. The necessary commitment to scientific research, which is essential as the basis for any defensible conservation plan, was made too slowly. The resultant socio-political turmoil was likely avoidable, at least in part, and the controversy would not have been so intractable if better scientific information had been available earlier.

Concerns about wildlife conservation in relation to forest management are limited neither to the Pacific Northwest nor to spotted owls. Appeals and legal challenges of timber management activities, relative to effects on wildlife, are now common throughout the country. The potential for re-enactment of the Pacific Northwest/old-growth. scenario exists throughout the western United States. And there is growing public sentiment that serious attention to the conservation of biological diversity is long overdue outside the Pacific Northwest.

PURPOSE

To address this situation, the USDA Forest Service decided in 1993 to evaluate what is known about the biology and ecology of several species or groups of species that are potentially sensitive to the effects of forest management, including the harvest of late-successional forests. This so-called *conservation assessment* process is directed at interior cutthroat trout, bull trout, Pacific salmon, forest owls (flammulated, boreal and great-gray), marbled murrelet, northern goshawk, and forest carnivores (marten, fisher, lynx, and wolverine). The forest carnivores are included in this group because of their relatively large area requirements, their association with late-successional forests, and the relative lack of information available for conservation planning. In addition, most of the geographic ranges of forest carnivores (about 65% for the marten and fisher) are found on public lands, and the marten, fisher, and lynx have been judged to be at medium to high-viability risk due to the reduction of old-growth forests in the Pacific Northwest (Thomas et al. 1993a, 1993b).

The conservation assessment process is intended to produce three specific products for each of the species in question: an overview of the existing state of knowledge with regard to species biology and ecology; a discussion of the management considerations stemming from this knowledge; and recommendations for research needed to fill voids in existing knowledge. Our mandate did not include the development of specific management recommendations and none appear here. The conservation assessment process is intended to lay the foundation for developing conservation strategies for species of concern. Thus, knowledge voids are assessed in this context, and the research recommendations are intended to address the information needed for developing scientifically defensible conservation strategies. Conservation strategies build on conservation assessments by incorporating new information that results from assessment recommendations and by prescribing specific conservation measures needed to ensure population viability and species persistence. Research designed to fulfill assessment recommendations will result in an understanding of the ecology of each species. Only then can we determine whether particular silvicultural practices are consistent with forest carnivore population persistence and whether they may be used to manage each species' habitat.

OVERVIEW

The developing paradigm of conservation biology forms the basis for the forest carnivore conservation assessment. And, as outlined in the contents, we have attempted to address those biological and ecological topics that are central to the issue of maintaining viable populations of the species in question. Each species account (Chapters 2-5) addresses what is known about population ecology and demography, behavioral ecology, habitat requirements, movement ecology, and community interactions. These classes of information are fundamental to conservation planning. Knowledge of habitat requirements is essential for understanding the resources needed for spe-

cies persistence. Community interactions mediate the use of these resources and hence must be understood for reliable conservation planning. Community interactions in the form of predator-prey relationships also can have a direct effect on population persistence. The vital rates of natality and mortality, along with an understanding of how the environment influences these rates, constitutes basic information for developing models of population persistence. And an understanding of how movement ecology relates to the potential connectedness of populations within metapopulation structures is equally basic to understanding population dynamics and estimating persistence probabilities. Finally, because behavior mediates all interactions between organisms and their environment, understanding fundamental behavioral patterns is important to understanding species' ecology. In each of these broad categories, we have also tried to identify areas where information basic to conservation planning is currently lacking.

It would be ecologically naive to assume that knowledge in any of the above areas could be extrapolated with equal validity to all populations across the geographic ranges of each forest carnivore species. Rather, we assume that ecotypic variation exists within these species. Although the amount of this variation is unknown, we stress its potential significance in formulating of conservation strategies. Accordingly, we have adopted an ecological stratification scheme (Appendix A) that we believe represents the major physiographic and ecological influences likely to effect ecotypic variation. Species distribution patterns are superimposed on this ecological stratification in Appendix B. For reasons presented above (see Chapter 7 for additional discussion), we have also used this framework to make geographically explicit research recommendations in Chapter 7. By doing this, we are stressing that important ecological differences may exist among species populations and we are also cautioning against overextrapolation of research results.

An important feature of our ecological stratification is the explicit delineation of important ecoprovinces that span the Canada-U.S. border. Forest carnivore populations in the United States represent the southern portions of species' ranges that are centered in Canada. This distribution pattern has important implications for conservation planning, and international cooperation in developing conservation strategies seems appropriate. The ecological framework provided here should facilitate such cooperation.

We have focused on the western U.S., exclusive of Alaska. The Tongass National Forest in Alaska is currently involved in important analyses of long-term species viability for marten and other species (Interagency Viable Population Committee-Iverson, pers. comm.). We have focused on the western conterminous United States because concerns about habitat reduction and landscape modification through management appear to be most urgent in this area. Moreover, all four forest carnivore species are sympatric in portions of this area, thus affording the opportunity for ecosystem studies that examine the common elements of their ecologies, including a common prey base.

THE QUANTITY AND QUALITY OF EXISTING INFORMATION

Research findings like those reviewed in this book must be evaluated in terms of the quantity and quality of information available on any given topic and for any given location. Such an evaluation should form the basis for judgments about the reliability and salience of information relative to decision-making or conservation planning (see Romesburg 1981 for a pertinent discussion). We have taken steps throughout this assessment to help the reader evaluate the quantity and quality of the information presented. There are at least six ways in which research results can be misleading or misinterpreted and thus misapplied in a conservation assessment. These are discussed below.

Geographic Limitations

Existing information may be the result of research conducted at only one or a few geographic locations. Research results from a specific geographic area may be unreliable or even misleading when applied to other locations. The risks associated with such extrapolations generally increase as distances increase and ecological conditions become increasingly dissimilar. This is equally true when numerous studies have been conducted in the same geographic location. Although numerous studies may add to the reliability or breadth of knowledge as it applies to the geographic area of investigation, multiple studies from the same or very similar study areas do little to increase the value of the resultant information relative to other geographic areas with different ecological conditions.

Extensive Information From Few Studies

While single studies may provide important knowledge, insight, or even understanding, multiple studies provide scientific corroboration of these results. Accordingly, reliable bodies of knowledge are usually based on well-documented concordance among results of independent investigations. It follows that a literature review based on 10 studies does not reveal as strong an information base as the same review based on 20 or more studies. This is equally true when one or a few studies cover many topics, as is the case in many natural history studies (especially of the thesis or dissertation genre). This situation leads to copious citations and the documentation of findings across a broad array of topics, sometimes creating the false impression of an extensive body of information.

Small Sample Sizes and/or Highly Variable Results

Small sample sizes are related to anecdotal information in that the resultant information may fail to represent a meaningful or common natural condition or event. And, when little is known about a species, this type of inherently unreliable information tends to be repeated and applied without the necessary qualifiers. For example, our knowledge about the denning habitat requirements for lynx is based on very few actual den sites. In spite of this, some authors will cite the studies involved and portray our knowledge on this topic as much more solid than it actually is. In many cases, this kind. of situation goes undetected by decision-makers or readers of review articles or management-oriented overviews. Similar problems occur when larger sample sizes reveal highly variable findings, which are! then reported as a simple mean value without appropriate statistical qualifiers and professional interpretation.

Ambiguous Parameters and Problems of Scale

Some parameters are inherently ambiguous, and conclusions based on data resulting from the measurement of such parameters can be misleading. For example, simple occurrence of animals in some habitat says little about habitat requirements, and even intensive measures of parameters like density can sometimes be misleading (Van Horne 1983). In spite of this understanding, observations of animals occurring in particular environments are sometimes incorrectly reported as indicative of specific habitat requirements or a lack thereof (see Chapter 7 for additional discussion). Similarly, a species may conduct different activities in different habitats, as in the case of foraging and denning habitats. These habitats may be strikingly different but both are essential. A general description of the habitat requirements of the species should consider the availability of each type and their spatial juxtapositions.

Problems of scale arise when individuals within populations are sampled and the resultant parameter estimates are applied to the entire species. This seemingly obvious and easily avoidable problem is quite common, especially when ecological results are applied or interpreted in a management context (Ruggiero et al. 1994).

Definition of Terms and Inappropriate Inference

The issue of old-growth forest as important habitat for forest carnivores is laden with philosophical and semantic problems that can hinder communication about habitat requirements. "Old-growth" is a stage of forest development characterized by large components (e.g., logs, snags, live trees) and structural complexity (e.g., vertical and horizontal). These attributes vary as a function of vegetation type, site conditions, and disturbance history. Thus, in general, old growth is a concept rather than a specific set of conditions. Old-growth characteristics develop gradually as forests mature, so that there is no specific threshold where mature stands become old growth. Thus, the characteristics of late-successional forests (including the oldest forests) are what interest us as habitat for forest carnivores. In order to focus on the structural and compositional features of forest habitats, we have chosen to use the term *late-successional* forests when referring to mature and older forests that possess the attributes listed above.

Our work requires the definition of three additional terms: fragmentation, dispersal, and den site. "Fragmentation" occurs when a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original (Wilcove et al. 1986:237). The process of 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). "Dispersal" is

important because it connotes the successful establishment (usually by juvenile animals) of a breeding territory in an area distant from the natal area. "Natal den sites" are important because they play a key role in recruitment by providing parturition sites. Inappropriate inferences about dispersal are made when authors confuse the long-distance movement capability of animals with their ability to successfully disperse. Inappropriate inferences about habitat requirements for denning are made when authors use the term "den" in reference to resting sites that are not associated with parturition or rearing of young. Similarly, there are important ecological differences between natal den sites (used for parturition) and other den sites that are used subsequent to parturition.

Inappropriate Methods

Using the wrong method to address the right question can result in inaccurate or incomplete answers. Questions about population structure and area requirements, for example, are germane to conservation planning. Information about area requirements is best obtained by well-designed (i.e., sufficient data over appropriately long time-periods) radio-telemetry studies. However, telemetry studies are expensive, and much information about the area requirements of forest carnivores has been derived from relocations of marked animals. There is an important distinction here with regard to the quality of resulting information. Similarly, questions about population structure have often been addressed by examining the carcasses of trapped animals. The quality of inferences from such data is questionable because the structure and dynamics of exploited populations differ from unexploited populations in ways that are poorly understood.

For the reasons discussed in this section, we have tried to provide a realistic view of the actual scientific knowledge base that forms the foundation of the species-account narratives. We have done this in each species account by including a tabular summary of existing studies by topic and including information on study location, duration, methodology, and sample size. Similarly, in Chapter 7 (table 1) we have represented the geographic distribution of existing knowledge for all 4 species in 10 topical areas of special importance to conservation planning. We have also asked the authors of each species account to provide their thoughts about management considerations that follow from the state of knowledge and to provide their recommendations about information still needed for develoment of conservation strategies for each species. In addition, we present a synthesis of these management considerations and information needs in Chapters 6 and 7, thus giving the reader two perspectives on these important aspects of the assessment.

MANAGEMENT CONSIDERATIONS AND INFORMATION NEEDS

As alluded to above, the state of scientific knowledge on forest carnivores carries with it certain implications for land management. Because the quantity and quality of information available for the western United States is limited, one such implication is that the conservation status of forest carnivores is itself uncertain. Thus, empirically based management strategies for species conservation cannot now be developed, and a significant commitment to research is needed.

This need for much additional information through research leads to a practical dilemma. Conservation planning draws on information from all aspects of a species' ecology. Accordingly, for little-studied (and difficult-to-study) species like the forest carnivores, the list of information needs is long indeed. And the need to replicate some studies to generate regionally generalizable information only expands the list of needed research. The dilemma, then, is how to be scientifically rigorous in prescribing needed research while also recognizing the practical limits of available resources and acknowledging real questions about the feasibility of collecting certain crucial information (e.g., vital rates for wolverine populations). Long lists of needed studies for even a single species are difficult to prioritize and often lead to a piecemeal approach to research whereby knowledge gaps persist. Problems of consistency and comparability arise, and studies are conducted on an opportunistic rather than a comprehensive and well-integrated basis.

Our solution to this problem is to avoid long "laundry lists" of needed research (although detailed information needs are included in each species account) in favor of a comprehensive, programmatic approach to producing the information needed for developing conservation strategies for forest carnivores. In reality, most well-designed studies address multiple objectives or multiple information needs. Thus, we believe that for each species a few highly integrated and comprehensive studies replicated in the geo-

graphic areas of concern will satisfy existing information needs for conservation planning (see Chapter 7 for additional discussion). We believe this approach will result in high levels of consistency, a comprehensive body of knowledge, and optimal use of available resources. Unfortunately, it will also take considerable time, expense, and effort. This should not, however, deter managers from developing conservative interim guidelines that will maintain future options.

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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 mam-

mals 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 habi-

tat 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 succession 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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Chapter 3

Fisher

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INTRODUCTION

Natural History

The fisher (*Martes pennanti*) is a medium-size mammalian carnivore and the largest member of the genus *Martes* (Anderson 1970) of the family Mustelidae in the order Carnivora. The genus *Martes* includes five or six other extant species. The fisher has the general body build of a stocky weasel and is long, thin, and set low to the ground. A fisher's head is triangular with a pronounced muzzle, its ears are large but rounded, and its eyes face largely forward (Douglas and Strickland 1987). Adult male fishers generally weigh between 3.5 and 5.5 kg and are between 90 and 120 cm long. Adult female fishers weigh between 2.0 and 2.5 kg and are between 75 and 95 cm long. The weights of adult females are more constant than those of adult males over the species' range (Powell 1993).

From a distance fishers often look uniformly black but they are actually dark brown over much of their bodies. Guard hairs on a fisher's tail, rump, and legs are glossy black while those on the face, neck, and shoulders are brown with hoary gold or silver tips (Coulter 1966). The undersurface of a fisher is uniformly brown, except for white or cream patches on the chest and around the genitals. These patches might be used to identify individuals (Frost and Krohn, unpubl. data; Powell, unpubl. data).

The fur of fishers is very soft and glossy but varies among individuals, sexes, and seasons. Males have coarser coats than females. The single yearly molt may begin during late summer and is finished by November or December (Coulter 1966; Grinnell et al. 1937; Powell 1985, 1993). During September and October, the guard hairs are noticeably shorter than during the rest of the year, giving fishers a sleek appearance.

Fishers have five toes on all four feet. Their claws are retractable but not sheathed. Fishers are plantigrade and their feet are large. There are pads on each toe and four central pads, one each behind digits 1, 2 and 3, 4, and 5, on each foot. From the central pads to the heels of the hindpaws, there are coarse hairs covering tough skin. The small, circular patches of coarse hair on the central pads of the hindpaws are associated with plantar glands and carry an odor distinctly different from other fisher odors (Buskirk at al. 1986; Powell 1977, 1981a, 1993). Because these patches enlarge on both males and females during the breeding season (Frost and Krohn, unpubl. data), as they do in American martens (*Martes americana*; Buskirk et al. 1986), they are probably involved in communication for reproduction.

Fishers leave a characteristic mustelid track pattern: two footprints next to each other but slightly out of line. Deep, fluffy snow and thin crusts restrict fishers' movements (Grinnell et al. 1937; Heinemeyer 1993; Leonard 1980b, 1986; Powell 1977; Raine 1983) and, to avoid deep snow, fishers sometimes hunt in habitats in which they can travel most easily rather than in habitats that have most prey (Leonard 1980b; Raine 1983, 1987). Distribution of deep winter snow may limit fisher distribution (Aubry and Houston 1992; Krohn et al., in press) and may affect success of reintroductions (Heinemeyer 1993) and perhaps reproduction (Krohn et al., in press).

At the time of European settlement, fishers were found throughout the northern forests of North America and south along the Appalachian and Pacific Coast mountains (Graham and Graham 1994). The northern limit to the range is approximately 60°N

latitude west of Hudson Bay and the latitude of the southern tip of James Bay to the east. Between 1800 and 1940, fisher populations declined or were extirpated in most of the United States and in much of Canada due to overtrapping and habitat destruction by logging (Brander and Books 1973; Irvine et al. 1964; Powell 1993). Closed trapping seasons, habitat recovery programs, and reintroduction programs allowed fishers to return to some of their former range (Gibilisco 1994; Powell 1993). Populations have never returned to the Southern Appalachians, and populations are extremely low in Oregon and Washington (the Pacific Northwest) and parts of the northern Rocky Mountains (Aubry and Houston 1992; Gibilisco 1994; Powell 1993).

In eastern forests, fishers occur predominantly in dense lowland and spruce-fir habitats with high canopy closure (Arthur et al. 1989b; Kelly 1977; Powell, 1994b; Thomasma et al. 1991, 1994). Aside from avoiding areas with little cover (Powell 1993), fishers use most forest types within extensive northern-conifer forests (Buck et al. 1983; Coulter 1966; Hamilton and Cook 1955; Jones 1991; Raine 1983) and within mixed-conifer and northern-hardwood forests (Clem 1977; Coulter 1966; Johnson 1984; Kelly 1977; Powell, 1994b; Thomasma et al. 1991, 1994). These mustelids occur in extensive, mid-mature, second-growth forests in the Midwest and Northeast (Arthur et al. 1989b; Coulter 1966; Powell 1993) but have been considered obligate late-successional mammals in the Pacific Northwest (Allen 1983; Harris et al. 1982). Later authors (Ruggiero et al. 1991; Thomas et al. 1993) have categorized the species as "closely-associated" with late-successional forests. Buck et al. (1983), Seglund and Golightly (1994, unpubl.), and Jones (1991) considered riparian areas important for fishers in California and Idaho. Although Strickland et al. (1982) suggested that fishers could inhabit any forested area with a suitable prey base, the distribution of fishers does not include the extensive southern forests of the eastern United States or the extensive conifer and mixed-conifer forests of the Rockies south of Wyoming (Powell 1993). Buskirk and Powell (1994) hypothesized that tree species composition is less important to fishers than aspects of forest structure which affect prey abundance and vulnerability and provide denning and resting sites. Such forest structure can be characterized by a diversity of tree sizes and shapes; light gaps and associated understory vegetation; snags; fallen trees and limbs; and limbs close to the ground.

Because fishers are generalized predators, their major prey are small- to medium-sized mammals, birds, and carrion (reviewed by Powell 1993). Wherever abundant, snowshoe hares (*Lepus americana*) are common prey. Other common prey include squirrels (*Sciurus* sp., *Tamiasciurus* sp., *Glaucomys* sp.), mice (*Clethrionomys gapperi*, *Microtus* sp., *Peromyscus* sp.), and shrews (*Blarina* sp., *Sorex* sp.). The porcupine (*Erethizon dorsatum*) is the fisher's best known prey but does not occur in fishers' diets at some locations due to low population densities. Carrion is eaten readily and is mostly that of large mammals, such as deer (*Odocoileus* sp.) and moose (*Alces alces*). Seasonal changes in diet are minor and sexual differences have not been found (Clem 1977; Coulter 1966; Giuliano et al. 1989; Powell 1993).

Newborn fishers weigh 40-50 g and are completely helpless; their eyes and ears are tightly closed (Coulter 1966; Hodgson 1937; LaBarge et al. 1990; Leonard 1986; Powell 1993). When 2 weeks old, kits are covered with light silver-gray hair and by age 3 weeks, kits are brown. By 3.5 weeks of age, white ventral patches may be visible. Their eyes open when 7-8 weeks old and teeth erupt through the gums at about the same age. Kits are completely dependent on milk until 8-10 weeks old. They cannot walk well until 8 weeks of age or older but by 10-12 weeks of age can run with the typical mustelid gait. From ages 10-12 weeks through 5-6 months, young fishers are the same general color as adults but are more uniform in color. Sexual dimorphism in weight between males and females is first apparent around age 3 months and is pronounced by late autumn (Coulter 1966; Hodgson 1937; Powell 1993).

Aggression between fisher kits begins at about 3 months of age (Coulter 1966; Powell 1993) but kits cannot kill prey until about 4 months of age. They do not require parental instruction to learn proper killing techniques (Kelly 1977; Powell 1977). Kits remain within their mothers' territories into the winter (Powell, unpubl. data), but most juveniles have established their own home ranges by age 1 year (Arthur et al. 1993).

Current Management Status

Fisher populations are formally protected in four western and northwestern states in the United States: Oregon, Utah, Washington and Wyoming (table 1). California and Idaho have closed their trapping seasons; California has not had an open season since

Table 1.--Current management status of fishers in the western United States and Canada.

Jurisdiction	Length of trapping season (weeks)	Year fishers reintroduced
Alberta	0-15	1990
British Columbia	0-20	
Manitoba		1972-73[1]
Northwest Territories	19-21	
Saskatchewan	17	
Yukon	17	
California	0[2]	
Idaho	0[2]	1962-63
Montana	4-9	1959-60, 1988-91
Oregon	Protected	1961[1]
Washington	Protected	
Wyoming	Protected	

[1] *Reintroduction failed.*
[2] *Fishers afforded protection through closed trapping season, but fishers are not afforded specific protected status.*

1945. Montana has had an open trapping season since 1983-84 with a quota of 20 animals; all trapped fishers were to be reported and tagged (table 1). Concern has been expressed about the status of fisher populations in Washington, Oregon, and California (Central Sierra Audubon Society et al. 1990; Gibilisco 1994; USFWS 1991) and the fisher is a candidate for "threatened" status in Washington. The fisher is considered a sensitive species by the Forest Service in all Regions where it occurs, with the exception of Region 6 (Appendix C, table 4b).

All of the western provinces and territories of Canada have open fisher trapping seasons and Alberta and British Columbia require that all trapped fishers be reported and tagged (table 1). In Ontario, the ratio of the number of juvenile fishers harvested to the number of adult females harvested in a given year is used to project next year's relative population size and allowable harvest (Strickland 1994). This technique is empirical, however, and therefore may not be applicable to other fisher populations.

Fisher populations are found in second-growth forests from northern Ontario and Minnesota eastward. Available information from the West (Aubry and Houston 1992; Buck et. al 1994; Jones and Garton 1994), however, suggests that fishers are late-successional associates in that region. This difference may reflect a response to forest structure rather than seral stage (Buskirk and Powell 1994; Powell 1993). Krohn et al. (in press) have argued, however, that the distribution of deep snow may be an overriding influence on habitat use, even in areas with adequate prey populations. Fishers in different regions may have different ecologies. Until the habitat relationships of fishers have been adequately studied in the West, we should be cautious about applying the results of studies conducted in the East to the conservation of fishers in the West.

DISTRIBUTION AND TAXONOMY

Range

Although the genus *Martes* is Holarctic in distribution, fishers are found only in North America. Their present range is reduced from their range before European settlement of the continent (Gibilisco 1994; Graham and Graham 1994; Hagmeier 1956), but most of this reduction has occurred in the United States. During historical times the northern limit to the fisher's range has been approximately 60° N latitude in the west and somewhat south of the southern tip of James Bay in the east, following the 15.5° C isotherm. Once fishers ranged from what is now northern British Columbia into central California in the Pacific coastal mountains and south into Idaho, Montana and probably Wyoming in the Rocky Mountains. In the western mountains of the United States fishers have been reported in the following ecoprovinces (see Appendix A and B): Georgia-Puget Basin, Thompson-Okanogan Highlands, Columbia Plateau, Shining Mountains, Northern Rocky Mountain Forest, Snake River Basins, Pacific Northwest Coast and Mountains, Northern California Coast Ranges, and Sierra Nevada. Within this range fishers have occurred most commonly in northwestern California (the Northern California Coast Ranges Ecoprovince), the southern Sierra Nevada Ecoprovince, and in northern Idaho and northwestern Montana (the Shining Mountains and Northern Rocky Mountain Forest Ecoprovinces) (Appendix B).

In what is now the central United States, fishers may have ranged as far south as southern Illinois (Gibilisco 1994; Graham and Graham 1990, 1994; Hagmeier 1956). And in the eastern part of the continent, fishers ranged as far south as what is now North Carolina and Tennessee in the Appalachian Mountains (Gibilisco 1994; Graham and Graham 1994; Hagmeier 1956). Fisher remains from southern Illinois to Alabama are probably artifacts created by the trading and travel patterns of American Indians (Barkalow 1961; Graham and Graham 1990).

Historical Changes in Populations and Distribution

During the last part of the 19th century and the early part of this century, fisher populations declined strikingly. Fishers were extirpated over much of their former range in the United States and in much of eastern Canada (Bensen 1959; Brander and Books 1973; Coulter 1966; deVos 1951, 1952; Dodds and Martell 1971; Dodge 1977; Hall 1942; Ingram 1973; Rand 1944; Schorger 1942; Weckwerth and Wright 1968). Human activities, especially trapping and logging, contributed substantially to these declines. Both are capable of reducing fisher populations today and information available about the past decline is inconclusive as to whether one cause was more important than the other. In addition, trapping and logging are not independent because logging increases access to forests by trappers.

Fishers are known by trappers to be easy to trap (Young 1975) and prices paid for fisher pelts, especially the silky, glossy pelts of females, have always been high. Before the 1920's, there were no trapping regulations for fishers and high fur prices provided trappers with strong incentive to trap fishers (Balser 1960; Brander and Books 1973; Hamilton and Cook 1955; Irvine et al. 1964; Petersen et al. 1977). Prices have never been stable, however, and have not been the same throughout the United States and Canada. Peak prices were paid for fisher pelts in 1920 and in the 1970's and 1980's; lowest prices were paid in the 1950's and 1960's (Douglas and Strickland 1987; Obbard 1987).

The decrease in fisher populations began first in the East, undoubtedly because of the longer history of European settlement. New York fisher populations had already begun to decrease by 1850 (Hamilton and Cook 1955), but the decrease in Wisconsin was not great before the first part of this century (Schorger 1942; Scott 1939). Wisconsin closed its fisher trapping season in 1921 but by 1932 the fisher was believed extinct in Wisconsin (Hine 1975). Fisher populations persisted in California, Oregon, and Washington (Aubry and Houston 1992; Schempf and White 1977; Yocum and McCollum 1973) but the last reliable reports of native fishers in Montana and Idaho came during the 1920's (Dodge 1977; Weckwerth and Wright 1968). Because of warnings from biologists, other states followed the example set by Wisconsin and closed their fisher-trapping seasons.

Fisher populations in Canada also showed significant declines but the declines were somewhat obscured by pronounced 10-year population cycles in response to cycles in snowshoe hare populations. The numbers of fishers trapped throughout the country declined by approximately 40% between 1920 and 1940 (deVos 1952; Rand 1944). Between 1920 and 1950 the number of fishers trapped in Ontario declined by 75%, adjusted to the phases of the 10-year population cycle (deVos 1952; Rand 1944). Fishers were completely exterminated from Nova Scotia before 1922 (Bensen 1959; Dodds and Martell 1971; Rand 1944).

At the same time that fishers were heavily trapped, their habitat was being destroyed. By the mid-19th century, clearing of forests by loggers and farmers and by frequent forest fires reduced the forested area of much of the northeastern United States to approximately 50%, from 95% 200 years earlier (Brander and Books 1973; Hamilton and Cook 1955; Silver 1957; Wood 1977). Land clearing in the Upper Midwest occurred during the early 20th century (Brander and Books 1973; Irvine et al. 1962, 1964). Either trapping or habitat destruction by itself could have dramatically reduced fisher populations; together, their effect was extreme. During the 1930's, remnant fisher populations in the United States could be found only on the Moosehead Plateau of Maine, in the White Mountains in New Hampshire, in the Adirondack Mountains in New York, in the "Big Bog" area of Minnesota, and in the Pacific States (Brander and Books 1973; Coulter 1966; Ingram 1973; Schorger 1942). In eastern Canada, the only remnant popular-tion was on the Cumberland Plateau in New Brunswick (Coulter 1966).

Concurrent with the closure of trapping seasons during the 1930's, the logging boom came to an end in eastern North America and abandoned farmland began to return to forest. The few remnant fisher populations in these areas recovered (Balser and Longley 1966; Brander and Books 1973). By 1949, wildlife managers in New York felt that the fisher population in that state had recovered sufficiently to reopen a trapping season. Over the following decades, trapping seasons were reinitiated in several states and provinces.

Following the reduction in fisher populations, porcupine populations climbed to extremely high densities in much of the forested lands in the United States (Cook and Hamilton 1957; Earle 1978). Porcupines were blamed for much timber damage (Cook and Hamilton 1957; Curtis 1944), though the damage was often exaggerated (Earle 1978). It is difficult to quantify the damage caused by porcupines be-

cause porcupines also beneficially prune trees (Curtis 1941). Nonetheless, damage did occur in areas with very high porcupine populations (Krefting et al. 1962). During the 1950's, interest in reestablishing fisher populations began to increase. Concurrent declines in the porcupine populations were noted in those areas of Minnesota, Maine, and New York where fisher populations were increasing (Balser 1960; Coulter 1966; Hamilton and Cook 1955). Cook and Hamilton (1957) suggested using fishers as a biological control for extremely high porcupine populations. Coulter (1966) warned, however, that there was no evidence that fishers could limit porcupine populations for long periods of time.

Nonetheless, during the late 1950's and 1960's, many states and provinces reintroduced fishers (table 1, Powell 1993). The purpose of these reintroductions was twofold: to reestablish a native mammal and to reduce high porcupine population densities (Irvine et al. 1962, 1964). Some states or provinces moved fishers within their borders, others released fishers from other jurisdictions. Not all releases succeeded in reestablishing fisher populations, but many did. A few states, for example Vermont and Montana, augmented low fisher populations. Massachusetts and Connecticut have reestablished fisher populations largely through population expansion from other states. And fishers have occasionally been sighted in Wyoming, North Dakota, South Dakota, and Maryland.

Thus, the range of the fisher in eastern North America has recovered much of the area lost during the first part of this century. The fisher is again living in areas from northern British Columbia to Idaho and Montana in the West, from northeastern Minnesota to Upper Michigan and northern Wisconsin in the Midwest, and in the Appalachian Mountains of New York and throughout most of the forested regions of the Northeast (Balser 1960; Banci 1989; Berg 1982; Bradle 1957; Coulter 1966; Earle 1978; Gibilisco 1994; Heinemeyer 1993; Irvine et al. 1962, 1964; Kebbe 1961; Kelly 1977; Kelsey 1977; Morse 1961; Penrod 1976; Petersen et al. 1977; Powell 1976, 1977a; Roy 1991; Weckwerth and Wright 1968; Williams 1962; Wood 1977). Many states and provinces have trapping seasons for fishers and regulations are adjusted in an attempt to maintain fisher populations at current levels.

In the 1980's and early 1990's, trapping mortality in southcentral Maine exceeded reproduction (Arthur et al. 1989a; Paragi 1990). Fishers have not returned to the southern Appalachians. Illinois, Indiana, and Ohio may never again have forested areas extensive enough to support fisher populations. And in areas where there has been extensive, recent logging that fragments forests extensively, fisher populations have not recovered, perhaps because fishers appear sensitive to forest fragmentation (Rosenberg and Raphael 1986). There were only 89 potential sightings of fishers in Washington between 1955 and 1993 and only 3 were supported with solid evidence, such as photographs or carcasses. Fishers may be on the verge of extinction in Washington (Aubry and Houston 1992; Aubry, unpubl. records). Although no evaluation of their status and distribution in Oregon has been conducted, sightings are extremely rare (Appendix B; Aubry, unpubl. data). Recent work with remote cameras, however, has detected the presence of fishers just west of the Cascade Crest in southern Oregon (S. Armentrout, pers. comm.). Finally, the fisher population in the southern Sierra Nevada Mountains in California (Appendix B) may be doing well, but it appears to be isolated from the population in northwestern California (W. Zielinski, pers. obs.). The latter population has remained stable since the early part of this century (Grinnell et al. 1937; Schempf and White 1977) and may have the highest abundance of all populations in the western United States.

It is sometimes necessary to augment isolated fisher populations with fishers captured elsewhere. Fishers have been released in eastern North America to reestablish populations where fishers had gone extinct. Releases have generally been unsuccessful in western North America. Roy's (1991) results indicate that many fishers from eastern North America may lack behaviors, and perhaps genetic background, to survive in western ecological settings. If fishers are moved from one population to another, inappropriate genetic background or ecotypic adaptations could have adverse effects on resident populations.

Irvine et al. (1962, 1964) recommended winter reintroductions. It has been believed, incorrectly, that females would not travel far as parturition approached (Roy 1991). Fishers reintroduced during winter travel long distances (Proulx et al. 1994; Roy 1991), however, and may be subject to greater risk of predation (Roy 1991) than they were in their capture sites.

Only once have fishers not been released during winter. Proulx et al. (1994) released fishers in the parklands of Alberta during both late-winter and summer. Fishers released during winter travelled significantly longer distances and had significantly higher mortality than the fishers released during

summer. Most fishers released in summer established home ranges close to their release sites, whereas this was not the case for the fishers released during winter. Proulx et al. recommended more experiments to find optimal release times; in the mean time, summer should be tried when possible.

Taxonomy

Goldman (1935) recognized three subspecies of fishers: *Martes pennanti pennanti*, *M. p. pacifica*, and *M. p. columbiana.* Recognition of subspecies, however, may not be valid. Goldman stated that the subspecies were difficult to distinguish, and Hagmeier (1959) concluded from an extensive study that recognition of subspecies was not warranted because the subspecies were not separable on the basis of pelage or skull characteristics. The continuous range of fishers across North America, allowing free interchange of genes, is consistent with a lack of valid subspecies. Anderson (1994) and Hall (1981) retained all three subspecies but failed to address Hagmeier's conclusion. On the basis of Whitaker's (1970) evaluation of the subspecies concept, Hagmeier was probably correct, but genetic analyses will be required to resolve this question.

Management Considerations

1. Isolated populations are of special concern and must be monitored.
2. Forest fragmentation may result in the isolation of populations.
3. Reintroductions would be most likely to succeed if translocated animals are from similar habitats in the same ecoprovince (Appendix A).

Research Needs

1. Develop, refine, and standardize survey methods to document the distribution of fishers in western North America.
2. Investigate the dispersal capabilities of fishers and characterize habitats and geographic features that facilitate or inhibit their movements, i.e., corridors and barriers.
3. Document genetic diversity within and among fisher populations to reevaluate named subspecies of fisher, to identify isolated populations that may require special management, and to identify similar genetic stocks for reintroduction.
4. Investigate factors that contribute to successful reintroductions and augmentations.

POPULATION ECOLOGY

Population Densities and Growth

Fisher population densities vary with habitat and prey, and density estimates in the northeastern United States have ranged from 1 fisher per 2.6 km^2 to 1 fisher per 20.0 km^2 (Arthur et al. 1989a; Coulter 1966; Kelly 1977). Coulter (1966) and Kelly (1977) did not believe that fishers could sustain densities of 1 fisher per 2-1/2-4 km^2 and Kelly reported a decrease in the number of fishers in New Hampshire and Maine following a period with such densities. Arthur et al. (1989a) calculated a summer density of 1 fisher per 2.8 to 10.5 km^2 in Maine and a winter density of 1 fisher per 8.3 to 20.0 km^2. The densities reported by Arthur et al. are the best available from the Northeast; they include seasonal changes in density caused by the spring birth pulse and they give the ranges of densities possible, showing the uncertainty of their estimates.

Information on fisher densities outside the Northeast is limited. Buck et al. (1983) estimated a density of 1 fisher per 3.2 per km^2 for their northern California study area. Fisher population densities in northern Wisconsin and Upper Peninsula Michigan have been estimated at 1 fisher per 12-19 km^2. (Earle 1978; Johnson 1984; Petersen et al. 1977; Powell 1977).

The density estimates for fisher populations vary for many reasons. Fisher populations fluctuate with populations of prey and in some places exhibit 10-year cycles in densities (Bulmer 1974, 1975; deVos 1952; Rand 1944) in response to 10-year cycles in snowshoe hare population densities (Bulmer 1974, 1975). Where fishers were reintroduced (e.g., Michigan, Wisconsin, Idaho, Montana), population densities may be low because of insufficient time for populations to build. Trapping in New England has at times been intense, even recently (Krohn et al. 1994; Wood 1977; Young 1975), and overtrapping can reduce populations in local areas (Kelly 1977; Krohn and Elowe 1993). Finally, it is difficult to estimate fisher population sizes because fishers do not behave according to the assumptions necessary to use most methods of estimating populations (e.g., equal trapability, no learned trap response, sufficient trapability to give adequate sample sizes). Therefore all estimates incorporate considerable sampling error.

W. Krohn (pers. comm.) suspects that as fishers colonize new, suitable habitat in Maine their density is initially very low, then rises to levels that probably cannot be maintained, and finally falls to intermediate levels. This pattern is consistent with information available from Wisconsin as well (C. Pils, pers. comm.). It is the pattern of population growth expected for animals whose density-dependent feedback comes through changes in adult and juvenile mortality rather than through changes in reproduction. Such a pattern is consistent with changes in fisher population density that track cycles in snowshoe hare numbers (Bulmer 1974).

This pattern of rapid population increase has not been observed in western populations, many of which have failed to recover despite decades of protection from trapping (e.g., northern Sierra Nevada, Olympic Peninsula), reintroductions (e.g., Oregon), or both. Therefore, one or more major life requisites must be missing. Suitable habitat may be limited, colonization of suitable habitat may be limited due to habitat fragmentation, or some other factor or combination of factors may be involved. Other populations, most notably the one in northwestern California (R. Golightly, pers. comm.; W. Zielinski, pers. obs.), have sustained themselves while nearby populations have apparently declined and failed to recover.

York and Fuller (in press) summarized the life history information available for wild and captive fishers (all of which came from eastern populations). Using a simple accounting model, they estimated the exponential rates of increase for a number of hypothetical populations. Initial values for survival and reproductive parameters were set at the lowest, weighted mean, unweighted mean, and highest values for each of four runs. Only the model run that incorporated the highest values of survival and reproduction resulted in lambda values that exceeded 1.0. The authors interpreted this to mean that most fisher populations require immigrants to increase and that only those with high reproductive and survival rates are self-sustaining.

Survivorship and Mortality

Fishers have lived past ten years of age (Arthur et al. 1992), which may be near the upper limit of life expectancy (Powell 1993). They exhibit low incidence of diseases and parasites (Powell 1993). Few natural causes of fisher mortality are known. Fishers have choked on food (Krohn et al. 1994) and have been debilitated by porcupine quills (Coulter 1966; deVos 1952; Hamilton and Cook 1955). Healthy adult fishers appear not to be subject to predation, except fishers that have been translocated. A fisher in Maine was trapped on the ice and killed by coyotes (*Canis latrans*, Krohn et al. 1994) and a fisher was killed by a dog (*Canis familiaris*) in Ontario (Douglas and Strickland 1987). An adult female fisher in northern California was killed by a large raptor, probably a golden eagle (*Aquila chrysaetos*) or great horned owl (*Bubo virginianus*, Buck et al. 1983). Reintroduction of fishers to the Cabinet Mountains of Montana was hindered by predation; of 32 fishers from Wisconsin released in the Cabinet Mountains, at least 9 were killed by other predators (Roy 1991). All appeared to have been in good health. It is possible that the differences between Wisconsin and Montana in habitat, topography, prey, and predators somehow made these fishers vulnerable to predation.

Trapping has been one of the two most important factors influencing fisher populations. Management of fisher populations, either to stabilize populations and harvests (Strickland 1994) or to provide recreational harvests, replaces natural population fluctuations with fluctuations caused by periods of overtrapping followed by recovery when trapping pressure decreases (Berg and Kuehn 1994; Douglas and Strickland 1987; Kelly 1977; Krohn et al. 1994; Parson 1980; Wood 1977; Young 1975; reviewed by Powell 1993). This occurs despite adjustments in trapping regulations. Fishers are also easily trapped in sets for other furbearers (Coulter 1966; Douglas and Strickland 1987; Young 1975). Where fishers are scarce, the populations can be seriously affected by fox (*Vulpes vulpes*, *Urocyon cinereoargenteus*) and bobcat (*Lynx rufus*) trapping (Coulter 1966; Douglas and Strickland 1987). Whether population fluctuations caused by trapping affect social structure of fisher populations in the same manner as natural population cycles is not known.

Mathematical models for the fisher community in Michigan (Powell 1979b) indicated that small increases in mortality due to trapping could lead to population extinction. Depending on the model, the increase in mortality needed to lead to extinction was as low as 3% or as high as 98%. This is equivalent to an increase in mortality of 1-4 fishers/km^2 above natural mortality levels. These models did not incorporate sex or age structure in the model fisher populations.

Based on data from radio-collared fishers, Krohn et al. (1994) estimated mean annual mortality rates

over a five-year period from a population in Maine where 94% of all mortality was from commercial trapping. The sexes did not show significant differences in survivorship for either adults or juveniles outside the trapping season, but adult females had significantly higher survivorship than adult males during the trapping season. It is not known whether the sexes have similar survivorships in populations that are not harvested. Survivorship during the trapping season for adult females, adult males, juvenile females, and juvenile males was 0.79, 0.57, 0.34, and 0.39, respectively. During the non-trapping season, survivorship rates were 0.87, 0.89, 0.75, and 0.71. Using a model that incorporated differential susceptibility to trapping for fishers of different ages and sex, Paragi (1990) found that annual fall recruitment needed to maintain a stable population was approximately 1.5 offspring per adult female (≥2 years old). Actual recruitment was 1.3 offspring per adult female, indicating a 2% per year population decline.

Age Structure and Sex Ratio

Age-specific survivorships for fisher populations appear to fluctuate with prey populations. During periods of high prey availability, juvenile fishers comprise a higher-than-average proportion of a trapped population; when prey populations are low and fisher populations decline, cohorts of old fishers comprise higher-than-average proportions of the population (Douglas and Strickland 1987; Powell 1994a). Harvested populations of *Martes* species tend to be biased more toward young animals, on the average, compared to unharvested populations (Powell 1994a). Average age structure for the heavily trapped fisher population in Ontario is highly skewed toward young animals (Douglas and Strickland 1987).

Our understanding of age structure in fishers and other animals is hampered by biases in population biology and demography research, which have historically been oriented to understand population stability (e.g., Lomnicki 1978, 1988; May 1973). Unstable age structure leads to variations in population responses to changes in prey populations. Because fishers do not reproduce until age two, populations biased toward young animals may not be able to respond to increases in prey populations as rapidly as populations biased toward old individuals. Thus, trapping may affect the abilities of fisher populations to respond to increasing prey populations (Powell 1994a). Natural fisher populations may be characterized by episodes of local extinction and recolonization (Powell 1993), which we have hypothesized to be the norm for weasel populations (*Mustela frenata, M. erminea, M. nivalis* [= *rixosa*]; Powell and Zielinski 1983). If remnant populations in the Pacific Northwest and Rocky Mountains are reduced in number and sufficiently separated they may not be capable of recolonizing depopulated areas.

Sex ratios of unharvested fisher populations are poorly known and true sex ratios (primary, secondary, or tertiary) are difficult to determine. Live-trapping and kill-trapping results for all mustelines exhibit a significant bias toward males (Buskirk and Lindstedt 1989; King 1975). Sex ratios for natural fisher populations should be close to 50:50 (Powell 1993, 1994b). This trapping bias toward males might skew harvested populations toward females (Krohn et al. 1994; Powell 1994b). This will not, however, necessarily increase reproductive output of the population. The density of adult males must be sufficient for maximal reproduction and recruitment must exceed mortality.

Management Considerations

1. The reproductive rates of fishers are low, relative to other mammals, and low density fisher populations will recover slowly.
2. Population densities of fishers are low, relative to other mammals, and can undergo fluctuations that are related to their prey. These fluctuations make small or isolated populations particularly prone to extirpation.
3. Fishers are easily trapped and can frequently be caught in sets for bobcats, foxes, coyotes, and other furbearers. To protect fisher populations, trapping using land sets may need to be prohibited. Incidental trapping of fishers in sets for other predators may slow or negate population responses to habitat improvement.

Research Needs

1. Obtain demographic data (age structure, sex ratio, vital rates) for representative, untrapped populations in ecoprovinces in the West.
2. Develop methods of estimating fisher densities.
3. Use demographic data and density estimates to develop models to estimate viable population sizes.

REPRODUCTIVE BIOLOGY

Reproductive rates

The reproductive biology of female fishers is similar to that of other members of the Mustelinae (weasels, martens, and sables) (Mead 1994). Female fishers are sexually mature and breed for the first time at 1 year of age (Douglas and Strickland 1987; Eadie and Hamilton 1958; Hall 1942; Wright and Coulter 1967). Ovulation is presumed to be induced by copulation and the corpora lutea of actively pregnant female fishers can be readily identified (Douglas and Strickland 1987; Eadie and Hamilton 1958; Wright and Coulter 1967). Implantation is delayed approximately ten months, and, therefore, female fishers can produce their first litters at age two. Females breed again approximately a week following parturition. Pregnancy rates for fishers are generally calculated as the proportion of adult females (≥2 yr) harvested whose ovaries contain corpora lutea (Crowley et al. 1990; Douglas and Strickland 1987; Shea et al. 1985). Corpora lutea generally indicate ovulation rates of ≥95% (Douglas and Strickland 1987; Shea et al. 1985), while placental scars indicate much lower birth rates.

Far fewer than 95% of female fishers ≥2 years old den and produce kits each spring. From 1984 to 1989, 12 radio-collared female fishers in Maine had a denning rate of only 63% (Arthur and Krohn 1991; Paragi 1990). Fifty percent (3 of 6) of the adult females in Massachusetts produced litters (York and Fuller, in press). Although an average of 97% of the female fishers from Maine, New Hampshire, Ontario and Vermont had corpora lutea (range 92 to 100), only 58% had placental scars (range 22-88; Crowley et al. 1990). This indicates that placental scars document birth of kits better than do corpora lutea (Crowley et al. 1990). A controlled study in Maine, however, is currently investigating the retention of placental scars in captive female fishers known to have produced litters (Frost and W. Krohn, pers. comm.). Why some females that have bred fail to produce litters is unknown, but nutritional deficiency related to stressful snow conditions is suspected because reproductive indices are higher in areas of low snowfall (Krohn et al., in press). Estimates of average numbers of corpora lutea, unimplanted blastocysts, implanted embryos, placental scars, and kits in a litter range from 2.7 to 3.9 (reviewed by Powell 1993). York and Fuller (in press) summarized the mean litter sizes for fishers from seven studies and discovered that they ranged from 2.00 to 2.90. Paragi (1990) estimated survival rates from six weeks until late October for kits in Maine to be ≥0.6 and estimated fall recruitment at 0.7-1.3 kits/ adult female.

Although it is usually assumed that sufficient numbers of males exist to breed with receptive females, this may not always be the case. Strickland and Douglas (1978; Douglas and Strickland 1987) found that trapping during January and February causes disproportionately high mortality of adult males, may decrease their numbers below that necessary to inseminate all females, and may even lead to population decline. In 1975 the fisher trapping season in the Algonquin region of Ontario was restricted to end on 31 December, reducing the trapping pressure on adult males. Thereafter, both the breeding rate of females and the population increased.

Breeding Season and Parturition

From mid-March through April, all adult males appear fully sexually active. Testes of fishers have been found with sperm as late as May (M. D. Carlos, Minn. Zool. Soc., unpubl. records; Wright and Coulter 1967). Despite having sperm, 1-year-old male fishers appear not to be effective breeders, probably because baculum development is incomplete. Beginning in March, adult male fishers, but not necessarily adult females, increase their movement rates and distances traveled (Arthur et al. 1989a; Coulter 1966; Kelly 1977; Leonard 1980b, 1986; Roy 1991). Established spacing patterns of adult males break down, they trespass onto the territories of other males, and they may fight (Arthur et al. 1989a; Leonard 1986). The first visible sign of estrus in female fishers is the enlargement of the vulva (Laberee 1941; Mead 1994) and females are in estrus for about 6-8 days (Laberee claimed only two days), beginning 3-9 days following parturition for adult females (Hall 1942; Hodgson 1937; Laberee 1941). Douglas and Strickland (1987) summarized the breeding season for fishers to be from 27 February to 15 April, based on known birth dates of captive litters, but this ignored the 3-9 day delay between parturition and breeding. Implantation can occur as early as January and as late as early April (Coulter 1966; Hall 1942; Hodgson 1937; Laberee 1941; Leonard 1980b, 1986; Paragi 1990; Powell 1977; Wright and Coulter 1967).

Parturition dates as early as February and as late as May have been recorded (Coulter 1966; Douglas 1943; Hall 1942; Hamilton and Cook 1955; Hodgson

1937; Kline and D. Carlos, Minn. Zool. Soc., unpubl. records; Laberee 1941; Leonard 1980b; Paragi 1990; Powell 1977; Wright and Coulter 1967). The only data from western North America are from fur farms in British Columbia, where parturition occurred during late March and early April (Hall 1942). Females probably breed within 10 days after giving birth. Thus, an adult female fisher is pregnant almost all the time, except for a brief period following parturition. Healthy females breed for the first time when they are 1 year old, produce their first litters when they are 2 years old, and probably breed every year thereafter as long as they are healthy.

Den Sites

Female fishers raise their young in protected den sites with no help from males. Almost all known natal dens (where parturition occurs) and maternal dens (other dens where kits are raised) have been discovered in eastern North America (Arthur 1987; Paragi 1990). Of these, the vast majority were located high in cavities in living or dead trees. This strongly suggests that female fishers are highly selective of habitat for natal and maternal den sites. Information is available for only two natal dens (California, Buck et al. 1983; Montana, Roy 1991) and one maternal den (California, Schmidt et al. 1993, unpubl.) in the western United States. The den found in Montana was in a hollow log 11 m long with a convoluted cavity averaging 30 cm in diameter. A natal den in California was in a 89 cm dbh ponderosa pine (*Pinus ponderosa*) snag. The maternal den was located in a hollow white fir (*Abies concolor*) log that was 1.5 m in diameter at the den site (Schmidt et al. 1993, unpubl.). Of the 32 natal dens found by Arthur (1987) and Paragi (1990) in Maine, over 90% were in hardwoods and over half were in aspens (*Populus* spp.). The den site Leonard (1980a, 1986) studied in Manitoba was also in an aspen. Because female fishers in eastern North America and in the Rocky Mountains are highly selective of habitat for resting sites (Arthur et al. 1989b; Jones and Garton 1994; Kelly 1977; Powell 1994b), they are probably highly selective of habitat for natal and maternal den sites as well.

Female fishers will use 1-3 dens per litter and are more likely to move litters if disturbed (Paragi 1990). The natal den found by Leonard (1980a, 1986) had no nesting material and was extremely neat after the kits left: no excrement, no regurgitated food, and no food remains. Natal nests of captive fishers are similarly spartan (Hodgson 1937; Powell, unpubl. data). A natal den found by Roy (1991), however, contained a dense mat of dried pine needles and moss. Roy also found a pile of 40-50 scats separated from the nest by 20 cm and behind a block in the cavity in the den log.

Except during mating, female fishers raised on fur farms spend little time outside natal nest boxes after parturition (Hodgson 1937; Laberee 1941). Although mating may keep a female away from her young for several hours when the young are only a few days old, she returns quickly to her young when she has finished mating. Wild female fishers exhibit individual variation in activity patterns both before and after weaning their kits. A female followed by Leonard (1980a, 1986) spent very little time away from her kits at first but spent increasingly more time away as they grew. Females followed by Paragi (1990) exhibited no discernable pattern. Kits are often moved from natal to maternal dens at 8 to 10 weeks of age (Leonard 1980b; Paragi 1990).

Scent Marking

During March fishers scent mark with urine, feces, musk, and black, tar-like marks on elevated objects such as stumps, logs and rocks (Leonard 1980b, 1986; Powell 1977). This March surge in scent marking coincides with the beginning of the breeding season as does the elaboration of plantar glands on the feet (Buskirk et al. 1986; W. Krohn, pers. obs.; Powell 1977, 1981a, 1993).

Fishers possess anal glands, or sacs, containing substances that have neither the strong nor offensive odor of weasels and skunks. The precise function of anal gland secretions is unknown. An odor and probably some secretion is discharged when wild fishers are frightened, such as when they are handled by humans (Powell 1993). In other mustelines, the anal gland secretions differ between males and females and change seasonally (Crump 1980a, 1980b). It is presumed that the anal gland secretions of fishers provide information to other fishers regarding sex, sexual activity, and perhaps maturity and territorial behavior.

Fishers lack abdominal glands (Hall 1926; Pittaway 1984), which are found in some but not all other *Martes* (de Monte and Roeder 1990; Rozhnov 1991). Other *Martes* have many glands on their cheeks, necks, and flanks (de Monte and Roeder 1990; Petskoi and Kolpovskii 1970). Fishers rub these areas, indicating that they may have glands there as well (R. Powell, pers. obs.).

Management Considerations

1. The recovery of fisher populations will be slow because fishers have small litters and do not produce their first litters until two year of age. Reproductive output of populations biased toward young fishers is limited by the inability of yearling males to breed effectively. Over-trapping may also bias the population toward young animals, further delaying recovery.

2. All natal and maternal dens in the West were found in large diameter logs or snags. These habitat elements may be reduced in stands that have been intensively managed for timber.

Research Needs

1. Determine characteristics of structures used as natal or maternal dens. Investigate whether den choices vary with the age of the kits and what factors influence a female's choice to change den sites over time.

2. Investigate the reproductive rates of fishers in free-living, non-trapped populations. In addition, study the reproductive rates of females in small populations because these may have suffered loss of genetic variability.

3. Determine the fisher mating system and whether few dominant males do most of the breeding. Determine whether the number of males, and sex ratio, affect the proportion of breeding females.

4. Test the hypotheses that successful hunting during winter leads to high implantation rates and that successful hunting during gestation leads to high embryo survival.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

Principal Prey Species and Diet

Fishers are generalized predators. They eat any animal they can catch and overpower, generally small- to medium-size mammals and birds, and they readily eat carrion and fruits (table 2). The methods used to quantify the diets of carnivores are at best indices of foods eaten. Food items with relatively large proportions of undigestible parts are overrepresented in gastrointestinal (GI) tracts and scats; therefore the remains of small mammals are over represented compared to large food items (Floyd et al. 1978; Lockie 1959; Scott 1941; Zielinski 1986).

A list of the foods identified from fecal remains or GI tract contents gives little information about where foods were obtained, when they were obtained, or how they were obtained. Almost all of the GI tracts collected for diet studies were obtained from trappers during legal trapping seasons and therefore only provide information on winter diets. Trap bait is commonly found in GI tracts of trapped animals, making it difficult to distinguish between kills initiated by fishers and items obtained as carrion. Trap bait, however, is a legitimate component of fishers' diets during the trapping season because fishers readily eat carrion (Kelly 1977; Powell 1993).

In the following discussion, we use the term "mice" to refer to all small cricetids, including microtines (voles and lemmings). All studies were predominantly winter diets (table 2). It is unfortunate that the only study of the food habits of fishers from Pacific Coast states was limited to the analysis of seven GI tracts from California and appears to have been affected by considerable sampling error due to small sample size. Grenfell and Fasenfest (1979) found a high frequency of "plant" material, a large amount of which was mushroom (false truffles). Black-tailed deer (*Odocoileus hemionus*), cattle, and mice remains also occurred in this sample.

The study of food habits of fishers in the Idaho Rocky Mountains (Jones 1991) has only slightly larger sample sizes: 7 GI tracts and 18 scats. Both GI tracts and scats had high frequencies of occurrence of mammal remains (58% and 68%) and low frequency of occurrence of bird remains (3%, 4%). Ungulate remains, consumed as carrion, were common in both samples (86%, 56%). Remains of insects and other invertebrates were uncommon and vegetation was consumed commonly but probably incidentally to eating prey or in attempts to escape live traps.

For fishers in the Cabinet Mountains of Montana, 50% of the prey remains found in 80 scats were from snowshoe hares (Roy 1991). Mice and other small rodents constituted the next most common prey. Porcupines constituted 5-10% of the prey items eaten and deer carrion constituted less than 5%. Roy (1991) believed that the importance of carrion was underestimated by his scat analyses because the fishers he studied used deer carcasses extensively on several occasions but no scats were collected in those areas.

Snowshoe hares are the most common prey for fishers and have been reported as prey in virtually

Table 2.--Food habits of fishers in five geographic locations. When there are three or more sources of information for a geographic location the range of frequencies of occurrence are provided and when there are only two sources of information commas separate the actual frequencies. The types of samples used are listed under each location.

Food item	California stomach	Idaho GI + scat	Maine New Hampshire New York GI + scat	Manitoba Michigan Minnesota stomach + scat	Ontario GI
Medium-sized prey					
Snowshoe hare	0	29, 50	3-28	19-84	12, 44
Porcupine	0	0, 6	0-26	0-20	20, 35
Small prey					
Mice and voles[15]	37	43, 39	3-50	3-20	9, 16
Shrews and moles[16]	12	0, 0	3-52	0-8	7, 8
Squirrels [17]	12	14, 33	9-25	1-14	0, 4
Birds	0	14, 17	6-30	0-8	11, 23
blue & gray jays	0-7	0	0, 2		
ruffed grouse	0-12	0-7	4, 14		
misc. & unident,[20]	0-19	0-9	2, 7		
Carrion					
White-tailed/black-tailed deer + moose + elk	25	86, 56	2-50	0-28	3, 22
Prey including trap bait					
Muskrat[18]	0	0, 0	0-9	0-1	0, 15
Raccoon[18]	0	0, 0	0-5	0	1, 3
Beaver[18]	0	29, 6	1-17	0	0, 2
Misc. & unident.					
Mammals[19]	100	14, 24	0-30	9-14	2, 45
Vertebrates[21]	88	0, 6	0-4	3-35	12, 13
Arthropods	37	0, 22	0-5	0-2	3, 21
Plant materlal[22]	100	39, 21	3-37	6-13	18, 61
Sources	1	2	3,4,5,6,7,8,9	10,11,12	13,14

' Grenfell and Fosenfest 1979.
[2] Jones 1991.
[3] Coulter 1966.
[4] Arthur et al. 1989o.
[5] Stevens 1968.
[6] Kelly 1977,
[7] Guiliano et al, 1989.
[8] Hamilton and Cook 1955.
[9] Brown and Will 1979,
[10] Roine 1987.
[11] Powell 1977,
[12] Kuehn 1989.
[13] De Vos 1952.
[14] Clem 1977.
[15] Clethrionomys, Microtus, Mus, Napeozopus, Peromyscus, Reithrodontomys, Synaptomys, Zopus.
[16] Blaring, Scolopus, Sorex.
[17] Glaucomys, Sciurus, Tomiasciurus,
[18] Includes bolt.
[19] Miscellaneous mammals (often bait): moles, cottontail rabbit, mink, red fox, American marten, weasels, otter, caribou, fisher, skunk, beaver, muskrat, woodchuck, domestic mammals, unidentified,
[20] Miscellaneous birds: red-breasted nuthatch, thrushes, owls, black-capped chickadee, downy woodpecker, yellow-shafted flicker, sparrows, dark-eyed junco, red-winged blackbird, starling, crow, ducks, grouse eggs, domestic chicken, unidentified.
[21] Miscellaneous vertebrates: snakes, toads, fish, unidentified,
[22] Plant material: apples, winterberries, mountain ash berries, blackberries, raspberries, strawberries, cherries, beechnuts, acorns, swamp holly berries, miscellaneous needles and leaves, mosses, club mosses, ferns, unidentified.

all diet studies (table 2). The species range of the snowshoe hare is coincident with almost the entire fisher species range and, therefore, snowshoe hares are expected to occur frequently in the diets of fishers. The occurrence of snowshoe hare remains in fisher scats ranges from 7% to 84% (table 2), though the California study (Grenfell and Fasenfest 1979) and a study in progress in Connecticut (Rego, pers. comm.) did not discover hare in the diet. Surprisingly, raccoon (*Procyon lotor*) are common prey in Connecticut. Fisher populations across Canada cycle in density approximately 3 years behind the hare cycle (Bulmer 1974, 1975) and as the snowshoe hare population declines, snowshoe hares decrease in fishers' diets (Kuehn 1989).

Understanding the habitat relationships of fisher prey is an important element of understanding fisher ecology. Fishers often hunt in those habitats used by hares (Arthur et al. 1989b; Clem 1977; Coulter 1966; Kelly 1977; Powell 1977, 1978; Powell and Brander 1977) and may direct their travel toward those habitats (Coulter 1966; Kelly 1977; Powell 1977). Hares use a variety of habitat types (Keith and Windberg 1978), but areas with sparse cover appear to be poor hare habitat (Keith 1966). Hares tend to concentrate in conifer and dense lowland vegetation during the winter and to avoid open hardwood forests (Litvaitis et al. 1985). On the Olympic Peninsula of Washington hares appear common in both early and late successional Douglas-fir forests stands, but not mid-successional stands (Powell 1991, unpubl.).

The fisher-porcupine predator-prey relationship has been the subject of considerable study. The importance of porcupines as prey for fishers is reflected in the evolution of the unique hunting and killing behaviors used by fishers to prey on porcupines. Their low build, relatively large body, great agility, and arboreal adaptations make them uniquely adapted for killing porcupines. As a result of these adaptations, fishers have a prey item for which they have little competition. The importance of this should not be underemphasized, even though fishers are found in areas with no porcupines.

Porcupines are important prey for fishers in many places and the frequency of porcupines in diet samples can reach 35% (table 2). Porcupines, however, are seldom as common in fisher diets as snowshoe hares and sometimes they are completely absent. Hares are preferred over porcupines (Powell 1977), presumably because hares are easier and less dangerous to catch. Nonetheless, where porcupines and fishers co-occur, fishers eat porcupines.

Collectively, mice appear in fishers' GI tracts and scats almost as frequently as snowshoe hares. White-footed mice (*Peromyscus leucopus*), deer mice (*P. maniculatus*), red-backed voles (*Clethrionomys gapperi*), and meadow voles (*Microtus pennsylvanicus*) are the most common mice found in fishers' diets and are generally the most common mice in fisher habitat. Mice are probably not as important to fishers as their occurrence in the diet samples indicates. Because they are small, have a relatively large amount of fur and bones, and are eaten whole, mice are overrepresented in the GI tracts and scats of fishers. Mice are often active on the surface of the snow during the winter, especially white-footed mice, deer mice, and red-backed voles (Coulter 1966; Powell 1977, 1978), where fishers presumably catch them more frequently than under the snow.

Shrews are found with unexpectedly high frequencies in GI tracts and scats of fishers, since carnivores are usually reluctant to prey on them (Jackson 1961). Shrews are often active during periods of extreme cold (Getz 1961) and, therefore, may sometimes be relatively abundant locally.

Squirrels are common mammals throughout the fisher's range but are eaten less frequently than mice. Red squirrels (*Tamiasciurus hudsonicus*), Douglas squirrels (*T. douglasii*), and flying squirrels (*Glaucomys* spp.) are found over more of the fisher's range and are, therefore, eaten more often than grey and fox squirrels (*Sciurus* spp.). Red squirrels are difficult to catch (Jackson 1961) and fishers probably catch them most often when they sleep in their cone caches. Fishers capture flying squirrels on the ground (Powell 1977) and in nest holes in trees (Coulter 1966). Because most food habits studies are conducted in winter, chipmunks (*Tamias* spp.) and other hibernating ground squirrels (*Spermophilus* spp., *Marmota* spp., and others) are probably underrepresented in the sample.

The remains of deer and other large ungulates have been found in all diet studies of fishers, but in most studies the total volume of deer remains was small in comparison to its incidence (Clem 1977; Coulter 1966; deVos 1952; Powell 1977). Fishers often return to carcasses long after all edible parts are gone and only tufts of hair and skin are left. Some fishers may have deer hair in their digestive tracts and scats almost all winter and still have eaten few meals of venison (Coulter 1966). Kuehn (1989) reported, however, that the amount of fat carried by fishers in Minnesota increased when the number of white-tailed deer (*Odocoileus virginianus*) harvested by hunters in-

creased. Fishers apparently scavenged viscera and other deer parts left by hunters. Kelly (1977), Roy (1991) and Zielinski (unpub. data) documented maternal or natal dens in close proximity to deer carcasses suggesting that females may select dens near carrion.

Some captive fishers eat berries (W. Krohn, pers. comm.) but others generally refuse to eat any kind of fruit or nut (Davison 1975). However, plant material has been found in all diet studies of fishers. Apples are eaten by fishers in New England, where orchards have regrown to forests, but apparently only when other foods are unavailable (W. Krohn, pers. comm.).

Diet Analyses by Age, Season, and Sex

Juvenile fishers eat more fruits than do yearlings or adults (Guiliano et al. 1989). Because juveniles are learning to hunt, they may often go hungry (Raine 1979) and turn to apples and other fruits to ward off starvation. Analyses of diet by season have found little change in diet through the winter (Clem 1977; Coulter 1966) but significant increases in plant material, especially fruits and nuts, in summer (Stevens 1968).

No consistent differences in diet exist between the sexes (Clem 1977; Coulter 1966; Guiliano et al. 1989; Kelly 1977; Kuehn 1989; Stevens 1.968; reviewed by Powell 1993). Anatomical analyses demonstrating that the skulls, jaws, and teeth are less dimorphic than their skeletons (Holmes 1980, 1987; Holmes and Powell 1994a) suggest that dietary specialization of the sexes is unlikely.

Foraging and Killing Behavior

Fishers studied in eastern North America have two distinct components to foraging behavior: search for patches of abundant or vulnerable prey, and search within patches for prey to kill (Powell 1993). Typical of members of the subfamily Mustelinae, fishers hunting within patches of concentrated prey frequently change direction and zigzag. This pattern has been used in dense, lowland-conifer forests where snowshoe hares are found in high densities and in other habitats with high densities of prey (Powell 1977). Between patches of dense prey, fishers travel nearly in straight lines, searching for and heading to new prey patches.

Within habitat patches with high densities of prey, fishers hunt by investigating places where prey are likely to be found (Arthur et al. 1989b; Brander and Books 1973; Coulter 1966; Powell 1976, 1977a, 1978, 1993; Powell and Brander 1977). Fishers will run along hare runs (Powell 1977, 1978; Powell and Brander 1977; Raine 1987) and kill hares where they are found resting or after a short rush attack (Powell 1978). Fishers seeking porcupine dens in upland hardwood forests travel long distances with almost no changes in direction (Clem 1977; Powell 1977, 1978; Powell and Brander 1977). These long upland travels often pass one or more porcupine dens, which fishers locate presumably using olfaction and memory (Powell 1993).

The hunting success rates for fishers are difficult to quantify but appear to be low. There were 14 kills and scavenges along 123 km of fisher tracks in Upper Peninsula Michigan, representing approximately 21 fisher days of hunting (Powell 1993). Seven scavenges were only bits of hide and hair having little food value and 2 kills were of mice (Powell 1993). Thus, the remaining porcupine kill, hare kill, 2 squirrel kills, and scavenging deer were the major results of 21 days of foraging.

Fishers kill small prey such as mice and shrews with the capture bite, by shaking them, or by eating them. They kill squirrels, snowshoe hares, and rabbits with a bite to the back of the neck or head (Coulter 1966; Kelly 1977; Powell 1977, 1978), but a fisher may use its feet to assist with a kill (Powell 1977, 1978). Porcupines are killed with repeated attacks on the face (Coulter 1966; Powell 1977a, 1993; Powell and Brander 1977).

Porcupines deliver quills to fishers but they seldom cause infections or other complications (Coulter 1966; deVos 1952; Hamilton and Cook 1955; Morse 1961; Pringle 1964). All mammals appear to react in the same manner to porcupine quills. Quills carry no poison or irritant and have no characteristics that should cause infection. They are, in fact, covered with a thin layer of fatty acids, which have antibacterial action (Roze 1989; Roze et al. 1990). Porcupines may have evolved antibiotic coated quills to minimize infections from self-quilling when they fall from trees (Roze 1989) or to train individual predators to avoid them and thus to minimize predation (G. Whittler, pers. comm.).

Rabbits, hares, and smaller prey are usually consumed in one meal. Fisher have been observed to cache prey they cannot eat, sometimes in the temporary sleeping dens (Powell 1977). Fishers usually sleep close to large items, such as a deer carcass or a

porcupine, or will pull a porcupine into a hollow log sleeping den (Coulter 1966; deVos 1952; Jones 1991; Kelly 1977; Powell 1977, 1993; Roy 1991).

Management Considerations

1. Snowshoe hares are a major prey item almost everywhere fishers have been studied, including the Rocky Mountains. If this is confirmed from studies elsewhere in the West, managing for hare habitat might benefit fishers if it is not at the expense of denning and resting habitat.

2. In late-successional coniferous forests the presence of high densities of snowshoe hares or porcupines indicates the potential for a fisher population.

Research Needs

1. Determine the seasonal diets of fishers in representative ecoprovinces (Appendix A) in the western United States. In particular, study whether snowshoe hares and porcupines are important fisher prey in the West.

2. Investigate the habitat associations of species found to be common fisher prey and determine how vulnerable they are to fishers in those habitats.

3. Determine whether the management of habitat for primary prey species will increase or decrease habitat suitability for fishers.

4. Investigate whether natal or maternal den choices are influenced by the availability of carrion.

HABITAT RELATIONSHIPS

General Patterns and Spatial Scales

Fishers occur most commonly in landscapes dominated by mature forest cover and they prefer late-seral forests over other habitats (Arthur et al. 1989b; Clem 1977; Coulter 1966; deVos 1952; Johnson 1984; Jones and Garton 1994; Kelly 1977; Powell 1977; Raine 1983; Thomasma et al.1991, 1994). In the Pacific states and in the Rocky Mountains, they appear to prefer late-successional coniferous forests (Buck et al. 1983; Jones 1991; Jones and Garton 1994; Raphael 1984, 1988; Rosenberg and Raphael 1986) and use riparian areas disproportionately more than their occurrence (Aubry and Houston 1992; Buck et al. 1983; Heinemeyer 1993; Higley 1993, unpubl.; Jones 1991; Jones and Garton 1994; Seglund and Golightly 1994, unpubl.; Self and Kerns 1992, unpubl.). However, in two studies, both in the Rocky Mountains, there were times of the year where young to medium-age stands of conifers were preferred (Jones 1991; Roy 1991). In eastern North America fishers occur in conifer (Cook and Hamilton 1957; Coulter 1966; Hamilton and Cook 1955; Kelly 1977), mixed-conifer, and northern-hardwood forests (Clem 1977; Coulter 1966; Kelly 1977; Powell 1977, 1978). Everywhere, they exhibit a strong preference for habitats with overhead tree cover (Arthur et al. 1989b; Buck et al. 1983; Clem 1977; Coulter 1966; deVos 1952; Johnson 1984; Jones 1991; Jones and Garton 1994; Kelly 1977; Powell 1977, in press; Raine 1983; Raphael 1984, 1988; Rosenberg and Raphael 1986; Thomasma et al. 1991, 1994).

Throughout most of the fisher's range, conifers constitute the dominant late-successional forest types. In the Northeast and Upper Midwest, fishers successfully recolonized and were successfully reintroduced into forests that are predominantly mid-successional, second-growth, mixed-conifer, and hardwood forests. This does not mean that all mid-successional, second-growth forests meet the requirements to support fisher populations. In the Idaho Rocky Mountains, fishers use predominantly old-growth forests of grand and subalpine fir (Jones and Garton 1994). In the Coast Ranges and west-side Cascade forests, fishers are associated with low to mid-elevational forests dominated by late-successional and old-growth Douglas-fir and western hemlock (Aubry and Houston 1992; Buck et al. 1983, 1994; Raphael 1984, 1988; Rosenberg and Raphael 1986). However, in east-side Cascade forests and in the Sierra Nevada fisher occur at higher elevations in association with true fir (*Abies* sp.) and mixed-conifer forests (Aubry and Houston 1992; Schempf and White 1977).

Fishers do not appear to occur as frequently in early successional forests as they do in late-successional forests in the Pacific Northwest (Aubry and Houston 1992; Buck et al. 1983,1994; Raphael 1984, 1988; Rosenberg and Raphael 1986). While some recent work in northern California indicates that fishers are detected in second-growth forests and in areas with sparse overhead canopy (Higley 1993, unpub.; R. Klug, pers. comm.; S. Self, pers. comm.), it is not known whether these habitats are used transiently or are the basis of stable home ranges. It is unlikely that early and mid-successional forests, especially those that have resulted from timber harvest, will provide the same prey resources, rest sites, and den sites as more mature forests.

Studies of fisher habitat have introduced a problem of scale that has not been resolved. Fishers occupy several regional biomes but have been studied most intensively in the forests in the eastern half of North America. Each population studied has been found within one large-scale habitat, such as mixed conifer and northern-hardwood forest or boreal forest. Studies have then investigated selection on the next smaller habitat scale: What stands within the major regional habitat do fishers use? On this scale it has been impossible to parcel portions of population survivorship and fecundity into different stand types. Researchers have therefore assumed that relative time or distance spent in stand types is a measure of habitat preference which, in turn, is a measure of fitness. However, this assumption may not always be true (Buskirk and Powell 1994). For example, fishers may find vulnerable, preferred prey more quickly in some habitats than others and thus may spend more time in habitats in which they find vulnerable prey more slowly (Powell 1994b). No studies have investigated large-scale habitat preferences, as might be found across the pronounced elevational gradients in the western mountains, yet fishers may have critical preferences on this large scale (Aubry and Houston 1992).

There is no universally appropriate scale for analyzing habitat because the scale used must match the questions being asked. Kelly (1977) found that the composition of forests used by a fisher population in New Hampshire was different from the selections made by individual fishers for forest types within their home ranges. Individual fishers appear to use different scales in choosing where to perform different behaviors (Powell 1994b). Where to establish a home range is decided on a landscape scale; where to hunt is decided on a scale of habitat patches; where to rest is decided on a scale of both habitat patches and habitat characteristics within patches. Habitat analyses can be done on several scales but confusing scales can lead to incorrect conclusions (Rahel 1990).

Forest Structure

Habitat requirements of fishers may not always coincide with habitat variables measured, such as predominant tree species and forest types. Buskirk and Powell (1994) hypothesized that physical structure of the forest and prey associated with forest structures are the critical features that explain fisher habitat use, not specific forest types. Structure includes vertical and horizontal complexity created by a diversity of tree sizes and shapes, light gaps, dead and downed wood, and layers of overhead cover. Forest structure should have three functions important for fishers: structure that leads to high diversity of dense prey populations, structure that leads to high vulnerability of prey to fishers, and structure that provides natal and maternal dens and resting sites. Examining fisher habitat use at this level may reconcile the apparently different habitat choices made by eastern and western fishers. Forest structure may also be important to fishers through effects on snow depth, snow compaction, and other snow characteristics (Aubry and Houston 1992; Heinemeyer 1993; Krohn et al., in press).

All habitats used disproportionately by fishers have high canopy closure, and fishers avoid areas with low canopy closure (Arthur et al. 1989b; Coulter 1966; Jones and Garton 1994; Kelly, 1977; Powell 1977, 1978; Raphael 1984; Rosenberg and Raphael 1986; Thomasma et al. 1991, 1994). Fishers also appear to select areas with a low canopy layer that occur in lowland habitat with dense overall canopy cover (Kelly 1977). Late-successional Douglas fir forests of the Pacific Northwest are characterized by multiple layers of cover that create closed-canopy conditions (Franklin and Spies 1991). The studies conducted in this region have concluded that fishers use late-successional forest more frequently than the early to mid-successional forests that result from timber harvest (Aubry and Houston 1992; Buck et al. 1994; Rosenberg and Raphael 1986). Similarly, fishers in the Rocky Mountain study preferred late-successional forests with complex physical structure, especially during the summer (Jones and Garton 1994). However, in areas where late-successional forests are characterized by more open conditions (e.g., ponderosa pine forests maintained by frequent light fires in the Sierra Nevada, McKelvey and Johnson 1992), it is uncertain if fishers will still prefer the closed canopy conditions typical of more mesic ecoregions.

Open, hardwood-dominated forests are frequently avoided throughout the fisher's range (Arthur et al. 1989b; Buck et al. 1983; Clem 1977; Kelly 1977) and, depending on the other available habitats, mixed hardwood-conifer forest types may be avoided (Buck et al. 1983, 1994; Coulter 1966).

Habitat and Prey

In western North America, our ability to characterize fisher foraging habitat on the basis of the habi-

tat of their prey is hampered by the absence of any significant food habitats studies. However, in the Upper Midwest and Northeast, dense lowland forests are preferred by snowshoe hares, and these habitats are selected by fishers. In the Pacific Northwest, the range of the snowshoe hare coincides with the original distribution of Douglas fir forests, where fishers appear to occur most frequently. On the Olympic Peninsula, snowshoe hare sign appears to be associated with late-successional, old-growth Douglas fir/western hemlock stands and with stands of Douglas fir and western hemlock regenerating from logging or from fire and having dense, low branches (Powell 1991, unpubl.). However, others have characterized the habitat of hares on the Olympic peninsula as "semi-open country with brush" (Scheffer 1949). The importance of snowshoe hare in the fisher diet and the habitat relationships of hare, in this region and elsewhere in the West, will need to be determined before the role of hare in fisher habitat choice can be understood.

In eastern North America hunting fishers use both open, hardwood and dense, conifer forest types (Arthur et al. 1989b; Coulter 1966; deVos 1952; Kelly 1977; Powell 1977, 1978; Powell and Brander 1977), but foraging strategies appear to be different in each habitat (Clem 1977; Powell 1977, 1978, 1981b, 1994b; Powell and Brander 1977). Fishers hunting in open, hardwood forests during the winter sometimes alter their directions of travel for small conifer stands where snowshoe hares are abundant (Coulter 1966; Kelly 1977; Powell 1977). Even though fishers may use certain habitats less than expected from their availabilities, those habitats may still have prey important for fishers. In Michigan, fishers used open, hardwood forest significantly less than expected by chance, yet porcupines were found exclusively in those forests. Fishers foraged in a manner that minimized the time and distance traveled in open, hardwood forests while maximizing their chances of finding vulnerable porcupines (Powell 1994b). Kelly (1977) found that fishers in New Hampshire selected habitats with the greatest small mammal (squirrels, shrews, mice) diversity but not the greatest small mammal populations, which are often found in open habitats avoided by fishers. Fishers are opportunistic predators and the availability of vulnerable prey may be more important than high populations of particular prey species.

Because fishers have relatively general diets their potential prey can occur in a variety of forest types and seral stages. However, fishers may forage in different habitats from the ones they use for resting and denning so a complete description of habitat requirements should consider both foraging *and* resting habitat needs. Resting and denning tend to occur in structures associated with late-successional conifer forests (see below), whereas prey can be distributed among a variety of successional stages. Because the types of forests that contain resting and denning sites may be more limiting, these habitats should be given more weight than foraging habitats when planning habitat management.

Snow and Habitat Selection

Fishers appear to be restricted to areas with relatively low snow accumulation. Deep, fluffy snow affects habitat use by fishers (Leonard 1980b; Raine 1983) and may affect distribution, population expansion, and colonization of unoccupied habitat (Arthur et al. 1989b; Aubry and Houston 1992; Heinemeyer 1993; Krohn et al. 1994). When snow is deep and fluffy, causing fishers to leave body drags, fishers move less but travel disproportionately often on snowshoe hare trails and on their own trails (R. Powell, pers. obs.). Fishers will even travel on frozen waterways, which they otherwise avoid, where the snow has been blown and packed by wind (Raine 1983). Where snow is deep, fishers may forage for hares on packed, snowplow drifts along roads that bisect hare habitat (Johnson and Todd 1985).

Snow appears to limit fisher distribution in Washington (Aubry and Houston 1992). On the Olympic Peninsula, and on the west slope of the Cascade Range (primarily the Pacific Northwest Coast and Mountains Ecoprovince, Appendix A), where snowfall is greatest at high elevations, fisher sightings in the past 40 years have been confined to low elevations. On the east slope of the Cascades, where snow is less deep, fisher sightings have been recorded at higher elevations. Krohn et al. (in press), using fisher harvest data, found that indices of fisher recruitment were lower in regions of Maine with deep and frequent snows compared to other areas.

Data from the Rocky Mountains are consistent with avoidance of deep, fluffy snow. Fishers in Idaho and Montana select flat areas and bottoms and avoid midslopes (Heinemeyer 1993; Jones 1991). However, fishers do not show detectable selection or avoidance of ridgetops and steep slopes (Heinemeyer 1993; Jones 1991), although the "selectivity indices" calculated

by Heinemeyer (1993) appear to confuse effects of small sample size with selection. The fishers in all three Rocky Mountain studies (Heinemeyer 1993; Jones 1991; Roy 1991) selected riparian areas, which have relatively gentle slopes, dense canopy, and perhaps protection from snow. Raines' (1983) research indicates that slopes with deep snow should provide poor footing for fishers and should be avoided.

The effect of snow on fisher populations and distribution may also help explain why fisher habitat appears so variable across the species' range. Where snow is deep and frequent, fishers should be expected to be either absent or occur where dense overhead cover intercepts the snowfall (Krohn et al., in press). This hypothesis may explain why fishers in the western United States and the Great Lakes region, where snow tends to be deep, are thought to occur most frequently in late-successional forests (Buck et al. 1994; Harris et al. 1982; Jones 1991; Thomasma et al. 1991) whereas second growth forests are more commonly used by fishers in the northeastern United States in areas where snowfall is relatively low (Arthur et al. 1989b; Coulter 1960). This effect, however, does not explain distribution among habitats during the summer. Additional work is necessary before we can understand how snow, and the interaction between snow and forest structure, influences fisher distribution and habitat choice.

Elevation

In the Pacific States, fishers were originally most common in low to mid-elevational forests up to 2500 m (Aubry and Houston 1992; Grinnell et al. 1937; Schempf and White 1977). In the past 40 years, most sightings of fishers on the Olympic Peninsula and the west slope of the Cascade Range in Washington have been at elevations less than 1000 m but sightings on the east slope of the Cascades where snow is less deep have generally been between 1800 and 2200 m (Aubry and Houston 1992). The highest elevation recorded for an observation of a fisher in California was 3475 m, in the Sierra Nevada (Schempf and White 1977), but most observations in northern California forests have been below 1000 m (Grinnell et al. 1937; Schempf and White 1977; Seglund and Golightly 1994, unpubl.; Self and Kerns 1992, unpubl.). In Montana, fishers released from Wisconsin avoided high elevations (1200-1600 m) and selected low elevations (600-1000 m) after they became established (Heinemeyer 1993).

Use of Openings and Nonforested Habitats

Fishers avoid nonforested areas (Arthur et al. 1989b; Buck et al. 1983, 1994; Coulter 1966; Jones 1991; Jones and Garton 1994; Kelly 1977; Powell 1977, 1978; Roy 1991). Fishers have avoided open areas 25 m across and less in the Midwest (Powell 1977). Large forest openings, open hardwood forests, recent clearcuts, grasslands, and areas above timberline are infrequently used in the West. Existing data are inadequate to assess the use of forest areas with intermediate forest cover resulting from either natural or human-caused disturbances.

Fishers are occasionally found in managed forests with little overhead tree cover, especially in northern California (R. Golightly, pers. comm.; M. Higley, pers. comm.; S. Self, pers. comm.), but the residency, age and reproductive status of these animals is unknown. It is possible that some of these observations may be of foraging animals, given that prey typically associated with nonforested habitats occur in the fisher diet (Jones and Garton 1994). Recently clearcut areas in the Northeast may be used during the summer, when they provide some low overhead cover from brush and saplings, but they are avoided during the winter (Kelly 1977). Rosenberg and Raphael (1986) listed fishers as an "area sensitive" species in northwestern California on the basis of a positive relationship in the frequency of their occurrence and the size of late-successional forest stands. This relationship suggests that, at least for northwestern California, as forested landscapes become more fragmented with openings fishers are less prevalent.

Aversion to open areas has affected local distributions and can limit population expansion and colonization of unoccupied range (Coulter 1966; Earle 1978). An area of farmland in Upper Peninsula Michigan delayed expansion of the population to the north by at least 15 years (R. Powell, pers. obs.) and the Pennobscot River delayed expansion of fishers to eastern Maine for over a decade (Coulter 1966).

Habitat Use by Sex, Age, and Season

There are few seasonal or sexual variations noted in the literature on habitat preferences of fishers. Female fishers in the Northeast may be less selective in their use of habitats during summer than during winter, especially for resting habitat (Arthur et al. 1989b; Kelly 1977). Male fishers in the mountains of

northern California may restrict access of females to preferred habitat that lack hardwoods (Buck et al. 1983). In Idaho, both sexes select late-successional conifer forests during summer but preferred young forests during the winter (Jones and Garton 1994). This was more likely due to a change in prey used during these seasons than to the influence of snow. Some change in habitat preference is caused by avoidance of open habitats that exist in winter but not in summer. Open habitat vegetated with young, deciduous trees and shrubs (typical of recently harvested areas in the East) can be used by fishers in summer (Kelly 1977) but are completely open with no overhead cover in winter.

Resting Sites

Fishers use a variety of resting sites. Most resting sites are used for only one sleeping or resting bout, but a fisher often will rest in the same site for many days, especially when it is close to a large food item, like carrion (R. Powell, pers. obs.), or during severe weather (Coulter 1966; deVos 1952; Powell 1977). Occasionally, individuals may use a site more than once (e.g., Jones 1991; Reynolds and Self 1994, unpubl.) and sometimes more than one individual will use the same resting site (Reynolds and Self 1994, unpubl.). Fishers often approach resting sites very directly, indicating that sites are remembered (deVos 1952; Powell 1993). Live trees with hollows, snags, logs, stumps, "witches' brooms," squirrel and raptor nests, brush piles, rockfalls, holes in the ground, and even abandoned beaver lodges have been reported as rest sites during various seasons (Arthur et al. 1989b; Coulter 1966; deVos 1952; Grinnell et al. 1937; Hamilton and Cook 1955; Powell 1977, 1993; Pringle 1964). The canopies of, or cavities within, live trees are the most commonly used rest sites reported in eastern and western studies (Arthur et al. 1989b; Buck et al. 1983; R. Golightly, pers. comm; Jones 1991; Krohn et al. 1994; Reynolds and Self 1994, unpubl.). In the published western studies, logs were of secondary importance, followed by snags (Buck et al. 1983; Jones 1991). The average diameters of trees used as resting sites were 55.8 cm in Idaho (Jones 1991), and 114.3 cm in northwestern California (Buck et al. 1983). Arthur et al. (1989b) located 180 rest sites of 22 fishers in Maine. Tree "nests" in balsam firs (resting sites on top of branches or in witches' brooms) were commonly used all year. Burrows, especially those of woodchucks (*Marmota monax*), were used most commonly in winter, and cavities in trees were used most commonly in spring and fall. This pattern of rest site use suggests that temperature affects resting site choice and that sites are chosen for warmth and insulation in winter and perhaps to prevent overheating in summer. This conclusion is also supported by the observation that fisher use of logs increases significantly during the winter in Idaho (Jones 1991).

During the winter, fishers sometimes use burrows under the snow with one or more tunnels leading 0.5 to 2.0 m to a larger, hollowed space under the surface of the snow (Coulter 1966; deVos 1952; Powell 1977). Arthur et al. (1989b) reported no use of snow dens by fishers in southcentral Maine, where snow is generally not deep. They did find that fishers tunneled up to 1.5 m through snow to get to ground burrows and they suggested that use of these snow dens may be exaggerated in the literature. Snow dens excavated in Upper Peninsula Michigan were not connected to ground burrows (Powell 1993).

Resting sites reported in studies in the western United States tend to occur predominantly in closed canopy stands. Jones (1991) analyzed canopy closure at 172 rest sites in Idaho and found that fishers preferred to rest in stands that exceeded 61 percent canopy closure during summer and winter, and avoided stands with less than 40 percent closure. Canopy closure at 34 rest sites in northcentral California averaged 82% (Reynolds and Self 1994, unpubl.).

Fishers are more selective of habitat for resting sites than of habitat for foraging. Researchers working in the Rocky Mountains, the Upper Midwest, and the Northeast in the United States have all found that fishers choose lowland-conifer forest types for resting significantly more often than for traveling or foraging (Arthur et al. 1989b; Jones and Garton 1994; Kelly 1977; Powell 1994b). As noted above, fisher prey may be found in a variety of forest types and seral stages. However, resting and denning tends to occur in large trees, snags and logs that are normally associated with late-successional conifer forests. Fishers in the eastern United States find these structures within some second-growth forests (Arthur et al. 1989b), but with the exception of a few observations of fishers using residual snags in early successional forest in California (S. Self, pers. comm.), there are no data in the West to determine how these components are used when they occur in other than late-successional stands. Because the types of forests that normally contain resting and denning sites may be more limiting than foraging habitat within the fisher

range in the West, they should receive special consideration when planning habitat management.

Management Considerations

1. In the western mountains, fishers prefer late-successional forests (especially for resting and denning) and occur most frequently where these forests include the fewest large nonforested openings. Avoidance of open areas may restrict the movements of fishers between patches of habitat and reduce colonization of unoccupied but suitable habitat. Further reduction of late-successional forests, especially fragmentation of contiguous areas through clearcutting, could be detrimental to fisher conservation.

2. Large physical structures (live trees, snags, and logs) are the most frequent fisher rest sites, and these structures occur most commonly in late-successional forests. Until it is understood how these structures are used and can be managed outside their natural ecological context, the maintenance of late-successional forests will be important for the conservation of fishers.

Research Needs

1. Replicate studies of habitat relationships within ecoprovinces (Appendix A) of the mountainous western United States.

2. Investigate the interaction between snow characteristics (depth, density, and frequency), elevation, and forest age/structure on distribution and habitat associations.

3. Determine whether resting and denning is limited to structures in late-successional forest stands.

4. Explore the importance of riparian areas to fisher habitat use in representative ecoprovinces.

5. After food habits studies are conducted, determine the habitat relationships of primary prey within ecoprovinces. Also, determine how forest structure mediates prey availability.

HOME RANGE

Fishers are solitary (Arthur et al. 1989a; Coulter 1966; deVos 1952; Powell 1977; Quick 1953) and appear to avoid close proximity to other individuals (Arthur et al. 1989a; Powell 1977). They probably maintain knowledge of the location of other individuals primarily via scent marking; however, direct contact and overt aggression has been documented (Arthur et al. 1989a; Coulter 1966; Kelly 1977; Leonard 1986; Powell 1977). The criteria fishers use when establishing a home range are unknown, but the density of vulnerable prey probably play an important role. Tracking data indicate that fishers use most intensively those parts of their home ranges that have high prey densities, and that these areas change (Arthur et al. 1989a; Coulter 1966; Powell 1977).

Home Range Size

Early estimates of fishers' home ranges from tracking data were substantially larger and less accurate than estimates derived more recently from radio-telemetry data (table 3). There is considerable variation in estimates of home range sizes, due in part to different researchers using different methods and treating data differently, in part to most methods of quantifying home ranges being inadequate, and in part to true variation. Recently developed fixed-kernel estimators quantify better than any other available methods both the outlines of home ranges and the distributions of use within home ranges (Seaman 1993; Silverman 1990).

Despite the limits of convex polygon and harmonic mean home range estimators, they have provided most of the information available about fishers' home ranges. There are no apparent geographical patterns in home range sizes, but male home ranges are larger than female home ranges (table 3). In table 3, we have calculated a mean home range area for each sex. Because methods were not consistent between studies, this figure can only be used for general comparisons and therefore includes no measure of variation. The mean home range size for adult male fishers is 40 km^2 (range 19-79), nearly three times that for females (15 km^2; range 4-32). This difference in size between male and female home ranges is greater than that expected from differences between the sexes in energy requirements, or food requirements, calculated from body size. Energy requirements are proportional to $W^{0.75}$, where W is a mammal's weight (McNab 1992). Because male fishers average slightly less than twice as heavy as females (Powell 1993), their energy requirements should be approximately 1.5-1.7 times greater than the energy requirements of females.

Because the territories of male fishers are large, hundreds of square kilometers of suitable habitat may be necessary to maintain sufficient numbers of males to have viable populations. Modeling popula-

tion viability is premature at this point. However, if a viable population has an effective size as small as 50 (Shaffer 1981), half of which is male fishers all of whom breed, then managed areas in the West may need to be at least 600 km^2 in California (based on Buck et al. 1983) to 2000 km^2 in the Rocky Mountains (based on Jones 1991) of contiguous, or interconnected, suitable habitat. Not all males and females breed, and minimal viable population size may be larger than 50. Therefore, managed areas likely need to be larger than these estimates. It is unknown whether the habitat is best distributed in an unbroken block, or, a dendritic pattern of wide and connected riparian areas.

There are several potential explanations (not mutually exclusive) for the disproportionate sizes of male and female home ranges. First, males may have energy requirements greater than expected from

Table 3.--Home range sizes (in km^2) estimated for fishers. Figures given are means ± standard deviations. The overall mean was calculated by using only one figure for each sex in each study (modified from Powell 1993).

Male	*N*	Female	*N*	Location	Method and comments	Source
20 ± 12	3	4.2	1	California	Convex polygons adults with >20 locations females all year males within the breeding season	Buck et al. 1983
23 ± 12	4	6.8	2	California	Convex polygons adults + juveniles females all year males within the breeding season	Buck et al. 1983
16 ± 6	2			California	Convex polygon biased to underestimate	Self and Kerns 1992
79 ± 35	6	32 ± 23	4	Idaho	90% harmonic mean adults + juveniles	Jones 1991
33 ± 25	7	19 ± 12	6	Maine	Convex polygon adults only May-December	Arthur et al. 1989a
27 ± 24	7	16 ± 12	6	Maine	90% harmonic mean adults only May-December	Arthur et al. 1989a
50 ± 40	7	31 ± 23	6	Maine	99% harmonic mean adults only May-December	Arthur et al. 1989a
35	1	15	1	Michigan	Convex polygon adults only winter	Powell 1977
85	2	17	7	Montana	Adaptive kernel non-breeding	Heinemeyer 1993
19 ± 17	3	15 ± 3	2	New Hampshire	Convex polygon adults only all year	Kelly 1977
26 ± 17	3	15 ± 6	3	New Hampshire	Convex polygon subadults only all year	Kelly 1977
23 ± 16	6	15 ± 5	5	New Hampshire	Convex polygon adults + subadults all year	Kelly 1977
49 ± 37	2	8 ± 4	5	Wisconsin	Convex polygon adults with >25 locations all year	Johnson 1984
39 ± 27	4	8 ± 4	7	Wisconsin	Convex polygon adults + juveniles all year	Johnson 1984
40	57	15	55		Mean	

body size and therefore need disproportionately larger home ranges. There is no support, however, for this hypothesis from laboratory research or field estimates of metabolic rates for fishers or other members of the subfamily Mustelinae (Buskirk et al. 1988; Casey and Casey 1979; Moors 1977; Powell 1979a, 1981b; Worthen and Kilgore 1981). Second, the actual areas used by males and females may be proportional to body size, though areas within home range outlines are not. Home ranges of male and female fishers do overlap extensively. In other mustelines, however, males spend minimal time within the home ranges of females encompassed within their own ranges (Erlinge 1977; Gerell 1970). No published data quantify the intensity of home range use by fishers. Third, males and females may space themselves to gain access to different resources: female priority is access to food whereas male priority is access to females. This has been shown to be the case for other mammals, including other mustelines (Erlinge and Sandell 1986; Ims 1987, 1988a, 1988b, 1990; Sandell 1986), and Sandell (1989) has hypothesized this to be the case for solitary carnivores, such as fishers. Fourth, males wander widely during the breeding season (Arthur et al. 1989a) and some of the data used to calculate the mean value for males includes these extra-territorial forays.

Monthly home range of males are greatly enlarged during the breeding season but home ranges of females are not (Arthur et al. 1989a; Johnson 1984). Because male fishers travel so widely during the breeding season, Arthur et al. (1989a) and Buck et al. (1983) excluded estimated locations made during the breeding season when they estimated home range sizes (table 3).

Seaman (1993) hypothesized that male and female mammals have equal lifetime reproductive costs. For male fishers, large body and home range sizes are reproductive costs. If these costs for males were equal to the high reproductive costs for females of raising litters, then home ranges sizes for males and females should be equal. Males, therefore, may forage less intensively throughout their home ranges. Monthly home ranges for fishers are significantly smaller than yearly home ranges and monthly home ranges of females tend to be smaller than those of males (Kelly 1977).

Territoriality

In most populations studied, including populations in California and Montana, fishers appear to exhibit intrasexual territoriality: home ranges overlap little between members of the same sex but overlap is extensive between members of opposite sexes (Arthur et al. 1989a; Buck et al. 1983; Heinemeyer 1993; Johnson 1984; Kelly 1977; Powell 1977, 1979a). Because territories of males are large, a male's territory may overlap territories of more than one female. How territories are maintained is not known. Little overt aggression has been documented between individuals and fishers undoubtedly communicate by scent marking. During the winter, fishers often walk along the tops of logs and large stumps and sometimes walk over and apparently drag their bellies and urinate on small stumps or mounds of snow (Leonard 1986; Powell 1977, 1993). Sometimes, during the breeding season, fishers leave black, tarry marks. These marks resemble feces resulting from rich meals of meat with little fur and bones but do not smell like feces. Fishers also urine mark at the entrances to resting sites and on large carcasses they are scavenging (Pittaway 1978, 1984; Powell, unpubl. data). When logs are moved from one individual's cage to another, the recipient will often rub its abdomen on the log (W. Krohn per. comm.).

Directed agonistic behavior has been observed between a captive adult female fisher and her young, among the young within captive litters five months old and older, and between two captive adult female fishers (Coulter 1966; Kelly 1977; Powell 1977). Arthur et al. (1989a) found male fishers with wounds, and Leonard (1986) examined the carcass of a male fisher with the canine of another fisher in its back.

Some researchers have suggested that intrasexual territoriality in carnivores occurs when large sexual dimorphism permits the two sexes to have different diets. However, this hypothesis has consistently been refuted for fishers, martens, and other mustelines (Clem 1977; Coulter 1966; Erlinge 1975; Holmes 1987; Holmes and Powell 1994; Kelly 1977; King 1989; Tapper 1976, 1979; reviewed by Powell 1994a). Patchily distributed prey is predicted to lead to low costs of sharing a territory with a member of the opposite sex (Powell 1994a). This cost is balanced by reduced chances of reproductive failure for males. Territorial behavior may not be a species-specific characteristic. From very low to very high prey population densities, the following pattern of change in fisher spacing is predicted (Powell 1994a):

transient → individual territories, decreasing in size → intrasexual territories, decreasing in size → extensive home range overlap.

Management Considerations

1. Fishers, especially males, have extremely large home ranges and the largest ranges may occur in the poorest quality habitat. The management of areas large enough to include many contiguous home ranges will probably have the best chance of conserving fisher populations.

Research Needs

1. Use fixed or adaptive kernel methods to determine home range sizes, and describe use areas therein, for males and females in representative ecoprovinces.
2. Evaluate the effects of prey densities and forest composition on home range size, shape, and composition.
3. Determine whether landscape features (i.e., topographic position, elevation within watershed) influence home range locations.

MOVEMENTS

Activity Patterns

Typical of mustelines, fishers have small numbers of activity periods (1 to 3) during a 24-hour period (Powell 1993). They are active day or night, when they are hungry or when their predominant prey is active (Powell 1993), but they often have peaks in activity around sunrise and sunset (Arthur and Krohn 1991) or during the night (deVos 1952). During all seasons, fishers are least active during midday and in winter fishers are often inactive in the middle of the night (Arthur and Krohn 1991; Johnson 1984; Kelly 1977). Fishers are most active during all daylight hours during summer and least active during winter (Johnson 1984; Kelly 1977). No significant difference in activity patterns has been noted between the sexes.

Movement Patterns

Fishers can travel long distances during short periods of time but travel, about 5-6 km per day on the average (Arthur and Krohn 1991; Johnson 1984; Jones 1991; Kelly 1977; Powell 1993; Roy 1991). Adult males are the most mobile, adult females are least mobile and subadults (<21 months old) of each sex are intermediate. All fishers travel longer distances during active periods in winter than in summer. Mobility of adult females appears to peak prior to parturition (Kelly 1977; Roy 1991) and then declines through the autumn months. The restricted mobility of females during summer may be caused by having dependent young and may explain why subadult females are more mobile than adult females.

All *Martes* species have clear adaptations for arboreality (Holmes 1980; Leach 1977a, 1977b; Sokolov and Sokolov 1971), partially due to their relatively unspecialized limb anatomy (Holmes 1980; Leach 1977a, 1977b). Fishers climb high into trees to reach holes and possibly to reach prey (Coulter 1966; Grinnell et al. 1937; Leonard 1980a; Powell 1977). Fishers in California were observed to travel from tree to tree to avoid dogs and hunters, sometimes leaping great distances from the branches of one tree to the branches of the next (Grinnell et al. 1937). Nonetheless, fishers are less arboreal than the popular literature claims (Coulter 1966; deVos 1952; Holmes 1980; Powell 1977, 1980; Raine 1987). In the Midwest and Northeast, almost all activity is terrestrial, and in boreal forests fishers may never climb trees while foraging (Raine 1987). Male fishers, who are significantly larger than females, are less adept at climbing (Pittaway 1978; Powell 1977).

Dispersal

Though independent from their mothers starting in the fall, young fishers do not disperse from their mothers' home ranges until mid to late winter (Arthur 1987; Arthur et al. 1993). At age 9 months, few juveniles have established their own home ranges but by age one year, most have (W. Krohn, pers. comm.). In most mammals, males disperse farther than do females and females may remain in or near their mothers' home ranges for their entire lives (Greenwood 1980). The data of Arthur (1987) and Paragi (1990) are not entirely consistent with this pattern because both males and females dispersed similar distances. Juveniles dispersed 10-16 km from their mother's range in Maine (Paragi 1990). In Idaho, two, 1-year-old males established ranges after moving 26 and 42 km, respectively. Because movements occur frequently along forested riparian areas (Buck et al. 1983; Heinemeyer 1993; Jones 1991), it is likely that dispersal occurs in these areas as well. Buck et al. (1983) thought that forested saddles between drainages were important linkages for fisher movements, although habitat selection during dispersal

has not been studied. Large open areas retard population expansion (Coulter 1966; Earle 1978), perhaps because dispersing individuals are inhibited from entering nonforested areas.

Movements and Reintroduction

Movements of reintroduced animals may provide an indication of the maximum distances that fishers from extant populations may move. In West Virginia (Pack and Cromer 1981), fishers moved an average of 43.7 km (90 km maximum) from the release site and movements as far as 98 km were noted in a Wisconsin reintroduction (Olsen 1966). In Montana, males and females moved up to 102 and 56 km (Weckwerth and Wright 1966) and up to 71 and 163 km (Roy 1991) from their release sites.

All fisher reintroductions except one were done during winter. Irvine et al. (1962, 1964) recommended winter reintroductions. Fishers can be trapped easily during winter and it was believed that females would not travel far as parturition approached. Nonetheless, fishers reintroduced during winter travel long distances (Proulx et al. 1994; Roy 1991) and may be subject to predation (Roy 1991).

Proulx et al. (1994) released fishers in the parklands of Alberta during both late winter and summer. Fishers released during winter traveled significantly longer distances and had significantly higher mortality than the fishers released during summer. Most fishers released in summer established home ranges close to their release sites, whereas this was not the case for the fishers released during winter. Proulx et al. recommended that more experiments be conducted to find optimal release times but that, in the mean time, fishers should be released in June when possible.

Management Considerations

1. Fishers are capable of moving long distances, but movements may be restricted in landscapes with large nonforested openings. The maintenance of contact between individuals and subpopulations and the recolonization of unoccupied habitat may be facilitated by reducing the size of openings.

2. Where reintroductions are necessary, conduct them during the summer until additional research dictates otherwise.

3. Fishers probably prey on snowshoe hares in the West. Where fishers are translocated to areas with cyclic snowshoe hare populations, release them during the increase phase of the hare cycle.

Research Needs

1. Investigate the seasonal movement patterns by adults of both sexes in representative ecoprovinces in the West.

2. Study the dispersal behavior of juvenile fishers. Evaluate the dispersal distances, the habitat characteristics (landscape and stand scales), and topographic features used and avoided during dispersal.

3. Test the hypothesis that dispersing juveniles are less selective of habitat than adults.

4. Investigate movements of fishers following translocation to understand how and where fishers establish home ranges.

COMMUNITY INTERACTIONS

Food Webs and Competition

The fisher, as a predator, is predominantly a secondary consumer. Occasionally, however, fishers eat berries and eat other carnivores making them both primary and tertiary consumers as well. In the community of organisms living in the northern forests of North America, fishers most clearly take the role of predators on small- to medium-size mammals and birds. Depending on the specific community, fishers may potentially compete with coyotes, foxes, bobcats, lynx (*Lynx canadensis*), American martens, wolverines (*Gulo gulo*), and weasels. Although this competition has not been documented and there is no direct evidence for its occurrence, the competitive interactions between fishers and American martens, in particular, have been the subject of some discussion.

Fishers and American martens are the only medium-sized, northern predators that are agile in trees and also are elongate and are able to explore hollow logs, brush piles and holes in the ground for prey. The geographic distributions of these species overlap considerably (Douglas and Strickland 1987; Strickland and Douglas 1978), but in the West martens tend to occur at higher elevations than fishers (Buskirk and Ruggiero, Chapter 2; J. Jones, pers. obs.; Schempf and White 1977). However, martens and fishers are sympatric in areas in the southern Sierra Nevada (W. Zielinski, pers. comm.) in northern Idaho (J. Jones pers. comm.), and undoubtedly in other areas as well. Fishers are larger than martens and are able to kill a larger range of prey. Whenever two gen-

eralized predators differ predominantly in size and lack specializations, the larger predator can prey upon the entire range of prey available to the smaller plus it can prey on larger prey. Thus, in periods of severe competition, the larger predator will prevail (Wilson 1975). However, where fishers and marten coexist it may be via niche partitioning (Rosenzweig 1966) because marten are small enough to be able to specialize on hunting voles, especially *Clethrionomys* sp., under snow (Buskirk 1983; Martin 1994). Clem (1977) found dietary overlap between fishers and martens in Ontario to be most profound during the winter but concluded that competition for food did not likely result in competitive exclusion. In the northeastern United States, Krohn et al. (1994) hypothesize that the inverse relationship between captures of fishers and martens by commercial trappers may result from an interaction between competitive displacement of marten by fisher and the avoidance of areas with deep and frequent snowfalls by fishers but not martens.

Fishers may compete with bobcats and especially lynx, because snowshoe hares are the fishers' predominant prey in many places. Presumably the foraging patterns used by fishers differ greatly enough from those used by the felids that competition is minimized. Fisher populations in Canada cycle in response to and about 3 years out of phase from snowshoe hare populations (Bulmer 1974, 1975). Fishers cycle 1-2 years out of phase from lynx (Bulmer 1974, 1975), because low hare populations affect fisher populations through increased juvenile and adult mortality but affect lynx populations primarily through increased juvenile mortality and decreased reproduction. However, these effects will be minimized in the United States where hare populations do not cycle (Dolbeer and Clark 1975; Koehler 1990). Fishers have been reestablished in areas inhabited by foxes, coyotes, bobcats, and lynx, which suggests that competition with these other predators is not limiting to fisher populations.

Where fishers and porcupines occur together, fishers have little competition with other predators for porcupines. Other predators do kill porcupines occasionally (Roze 1989) and mountain lions (*Puma concolor*) may kill porcupines more than occasionally (Maser and Rohweder 1983). Fishers, however, have unique adaptations for killing porcupines and no other predators have been implicated as regulators of porcupine populations (Powell 1977, 1993; Powell and Brander 1977; Roze 1989).

Predation on Fishers

As far as is known, adult fishers are not regularly subject to predation. The occasional fishers reported as killed by other predators were probably ill, old, otherwise in poor health, or lacking in appropriate behavior, making them easy and not dangerous to kill. Four of 20 radio-collared fishers in California died of wounds inflicted by predators or other fishers (Buck et al. 1983). Two fishers were killed by mountain lions in California (Grinnell et al. 1937) and 3 of 21 animals studied by Jones (1991) were killed by predators. Heinemeyer (1993) and Roy (1991) reported high predation rates on fishers translocated from Minnesota and Wisconsin to northwestern Montana. Predators there included bears (*Ursus* spp.), coyotes, golden eagles, lynx, mountain lions, and wolverines. The introduced fishers may have been at risk due to their unfamiliarity with the predators, forests, topography, snow conditions, and prey in the western mountains.

Although Heinemeyer's and Roy's results may give little insight into predation on fishers under natural conditions, their results give significant insight into design of reintroductions. Special steps may be necessary when fishers are released into habitat very different from that in which they were captured, especially when the new habitat supports several predators not known to the fishers in their original habitat. If fishers are released in summer, as suggested by Proulx et al. (1994), they may not travel long distances exposing themselves to other predators. When movements are reduced, fishers establish home ranges promptly and probably learn important local landscape features quickly. Fishers can be released into holding cages where they are housed for an habituation period, but Heinemeyer (1993) found that such "soft" releases in early winter did not affect subsequent movements and activity by released fishers. Alternatively, fishers might be released into areas with low populations of other predators, especially mountain lions and golden eagles.

It is possible that forest fragmentation may affect predation on fishers by other predators. If fragmentation causes fishers to travel long distances through unfamiliar habitat (especially unpreferred habitat) in search of mates, the fishers might be subject to predation.

Management Considerations

1. Animals reintroduced from the same, or nearby, ecoprovinces and into areas with low populations of

potential fisher predators have the best chance of survival.

2. Until the importance of competition between fisher and American marten is determined, it appears that management for both species on the same areas may not be as successful as exclusive areas for each species.

Research Needs

1. Test the hypothesis that the fragmentation of late-successional forest habitat changes competitive interactions between fishers and their potential predators and competitors.

2. Investigate the niche relationships of marten and fisher where they co-occur and test the hypothesis that snow depth and forest structure mediates competitive interactions.

3. Snowshoe hares may constitute a large proportion of the diet of fishers and lynx. Study the food habits of fishers and lynx where they occur together to assess the potential for direct competition.

CONSERVATION STATUS

Human Effects on Fishers

Humans and fishers interact in a number of ways. First, since before European colonization of North America, fishers have been valued for their pelts (Barkalow 1961; Graham and Graham 1990). Fishers have been trapped for fur and, to a lesser extent, farmed for fur. Second, humans affect fisher populations through forestry practices and other activities that alter the fishers' habitat. Fishers lose resting, denning, and foraging habitat through logging of late-successional forests, clearing of forests for agriculture, and clearing of forests for development. Third, fishers have been used to manage porcupine populations. And, fourth, the fisher is unique to North America and is valued by native and nonnative people as an important member of the complex natural communities that comprise the continent's northern forests. Fishers are an important component of the diversity of organisms found in North America, and the mere knowledge of the fisher's existence in natural forest communities is valued by many Americans. Fishers and their pelts are an important element of some American Indian cultures. For example, on the Hoopa Reservation in northwestern California skins are used to fashion quivers and skirts that are important ceremonial regalia, and the needs of fisher are considered in forest management (M. Higley, pers. comm.).

The fisher's reaction to humans in all of these interactions is usually one of avoidance. Even though mustelids appear to be curious by nature and in some instances fishers may associate with humans (W. Zielinski, pers. obs.), they seldom linger when they become aware of the immediate presence of a human. In this regard, fishers generally are more common where the density of humans is low and human disturbance is reduced. Although perhaps not as associated with "wilderness" as the wolverine (V. Banci, Chapter 5), the fisher is usually characterized as a species that avoids humans (Douglas and Strickland 1987; Powell 1993).

Trapping

Trapping, with logging, has had a major impact on fisher populations. Fishers are easily trapped and the value of fisher pelts in the past created trapping pressure great enough to exterminate fishers completely from huge geographic areas. Wherever fishers are trapped, populations must be monitored closely to prevent population decrease. In addition to the clear evidence from past population declines, there is evidence from more recent changes in populations in eastern states and provinces (Douglas and Strickland 1987; Kelly 1977; Krohn et al. 1994; Parson 1980; Strickland and Douglas 1978; Wood 1977; Young 1975) and theoretical evidence (Powell 1979b) that small changes in mortality due to trapping can greatly affect fisher populations.

Because fishers are easily trapped, where fisher populations are low they can be jeopardized by the trapping of coyote, fox, bobcat, and marten (Coulter 1966; Douglas and Strickland 1987; Jones 1991; Powell 1993). Wisconsin designated fisher wildlife management areas in the Nicolet and Chequamegon National Forest (approximately 550 km^2 and 1,000 km^2) where land sets for all furbearers were prohibited (Petersen et. al. 1977). During the two years that British Columbia closed the fisher season the incidental capture of fishers exceeded the legal capture the preceding year (V. Banci pers. comm.). The closure of all commercial marten trapping where their range overlaps that of the fisher in Washington and Oregon has been recommended by the Forest Ecosystem Management Assessment Team in a recent EIS (USDA 1994) until the rate of incidental take is considered

to be insignificant. Idaho and Montana each provide modest financial incentive for information about incidentally captured fishers (B. Giddings, pers. comm.; G. Will, pers. comm.). Where commercial trapping of terrestrial carnivores occurs, the threat exists that fishers will be trapped and that their populations could be negatively affected (Powell 1979b).

Forest Management

The extensive, clearcut logging done during the 1800's and early 1900's, together with trapping, decimated fisher populations all over the continent. Because fishers are associated most frequently with relatively unfragmented, late-successional forests, recent clearcut logging continues to affect fisher populations today through its profound effects on forest landscapes. Large nonforested areas are avoided by fishers, especially during the winter, and the fact that extensive areas of the Pacific Northwest have been recently clearcut (e.g., Morrison 1988) may be the reason fisher populations have not recovered in some parts of this region (Aubry and Houston 1992).

The problem for fishers is not with forest openings per se. Fishers evolved in forests where windthrow and fire were common. Small patch cuts, group selection harvests, and small clearcuts can superficially resemble both these disturbances in form and in the pattern of succession that follows. Fishers have been reported to use recently clearcut areas during the summer, when the cover formed by ground vegetation and young trees is dense, and, in the East, they also use young, second-growth forests. Presumably, fishers experience habitat loss when timber harvest removes overstory canopy from areas larger and more extensive than natural windthrow and fire would. Provided there are large patches of late-successional conifer habitat nearby, fisher populations should be able tolerate incidents of stand-replacing disturbances. Small patch cuts interspersed with large, connected, uncut areas should not seriously affect fisher populations. In fact, these small-scale disturbances may increase the abundance and availability of some fisher prey. Large clearcuts and numerous, adjacent, small clearcuts of similar age should seriously limit resting and foraging habitat for fishers during the winter. This, in turn, may limit fisher population size. The effect of uneven-aged timber management practices on fisher habitat have not been studied but are likely to have less effect on fisher habitat than even-aged management. Forestry practices aimed at maximizing wood production and minimizing rotation times will probably have detrimental effects on fisher populations.

For many species, including the fisher, much still needs to be known about how natural populations function. Differences in forest habitats between the Pacific States, the Rocky Mountains, and the forest of the Upper Midwest and Northeast are profound enough to prevent simplistic extrapolations about fisher-habitat relationships. We must learn how fishers use the forests of the western mountains before we can fully understand the components of these forests that are important to fishers.

Conservation Status in the Western United States

The primary reason for concern about the fishers in the western mountains of the United States is the utter lack of data on the ecology of the species. Only two intensive, radio-telemetry based habitat studies have been published on fishers, one in northwestern California (Buck et. al. 1983) and the other in Idaho (Jones 1991) (table 4). Two additional studies have been completed at about the same locations in Montana (Heinemeyer 1993; Roy 1991) but both individuals studied fishers that were introduced from Wisconsin and Minnesota. Inferences from these studies to extant populations elsewhere in the West may be limited. Only two natal dens and one maternal den have been discovered and described in the West (two of the three were in northwestern California). Only about 100 scats and gastrointestinal tracts have been examined to describe food habits, the majority of which may be unrepresentative of native fisher diets because they came from transplanted individuals in Montana (table 4). Thus, the quantity of data on the ecology of fishers in the West is extremely low. A sizeable amount of unpublished data exist (noted throughout the text above and in Appendix C) but the quality of this information is hard to verify and thus its usefulness is limited. Neither of the studies of native populations have been replicated within their ecoprovinces and entire ecoprovinces (see Appendix A) are without a single representative study (e.g., Georgia-Puget Basin, Pacific Northwest Coast and Mountains, Sierra Nevada, Columbia Plateau, Northern Rocky Mountain Forest). New research is underway in northern California (Reynolds and Self 1994, unpubl.; Seglund and Golightly 1994, unpubl.; Schmidt et al. 1993, unpubl.) and the southern Sierra

Table 4.--The knowledge base for the fisher 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 four studies (*) are represented in this table.

Topic, author	Location	Method	Duration (years)	Sample size
Home range & habitat use				
*Bucket al, 1994	California	Telemetry-convex polygon	1.5	6
*Heinemeyer 1993[1]	Montana/Idaho[2]	Telemetry-adaptive kernel	2	9/10[6]
*Jones 1991	Idaho	Telemetry-harmonic mean	4	10
*Roy 1991[1]	Montana[3]	Telemetry-habit use primarily	2	18
Demography				
Roy 1991[1]	Montana	Mortality and reproduction of transplanted animals	4	32
Food habits				
Grenfell & Fasenfest 1979[4]	California	GI tracts	-	8
Jones 1991	Idaho	GI tracts + scats	4	25
Roy 1991[1]	Montana	Scats	2	80
Dispersal[5]				
Natal dens				
Roy 1991[1]	Montana	Telemetry	2	1
Bucket al. 1983[6]	California	Incidental to study	-	1

[1] Data collected from transplanted individuals.
[2] Adaptive kernel home range calculated from Jones' (1991) data included.
[3] Same locations as Heinemeyer (1993).
[4] From fishers that died during the course of the study by Buck et al. (1983).
[5] No data for western fishers.
[6] Buck et al. (1983) same as Buck et al (1994).

Nevada (W. Zielinski, pers. comm.), but a tremendous amount of additional research is necessary before a responsible conservation strategy can be assembled.

A second reason for concern comes from interpreting the results of the two published studies on native populations in the West. In each case, fishers prefer late-successional coniferous forests: throughout the year in California (Buck et al. 1983) and especially in summer in Idaho (Jones 1991). Late-successional forests provide important benefits for fishers, especially resting and denning habitat. The reduction in this habitat and its increasing fragmentation is part of the reason fishers in the Pacific States are considered by many to be threatened with extirpation and why some have petitioned the U.S. Fish and Wildlife Service to list the fisher under the Endangered Species Act (Central Sierra Audubon Society et al. 1991).

Reintroductions appear not to have augmented populations in western Oregon and recent records of fishers in Washington are uncommon. Since the late 1950's, only one sighting of a fisher has been substantiated on the Olympic Peninsula in Washington, and that was a fisher killed in a trap in 1969. A fisher killed in the 1990-91 trapping season and a fisher trapped and photographed in 1993 in the Cascade Range are the only other substantiated reports (Aubry and Houston 1992; Aubry, unpub. records). Fishers are probably extirpated on the Olympic Peninsula and are either extirpated or very patchily distributed in meager populations in the rest of western Washington and Oregon.

It is our opinion that the precarious status of the fisher population in Washington and Oregon is related to the extensive cutting of late-successional forests and the fragmented nature of these forests that still remain. Fishers appear sensitive to loss of contiguous, late-successional Douglas fir forests in the Pacific Coast Ranges, west slope of the Cascade Range, and west slope of the Sierra Nevada (Aubry and Houston 1992; Gibilisco 1994; Raphael 1984, 1988; Rosenberg and Raphael 1986), but their habitat associations in more xeric forest types in the Pacific States (e.g., east slope of the Cascades, ponderosa pine forests in the Sierra Nevada) are unknown. We suspect that in Douglas fir forests, late-seral conditions provide the physical structure that allows fishers to hunt

successfully and to find suitable resting and denning sites. Young, second-growth forests may be unable to provide these requirements.

Establishing the reasons for the precarious status of the fisher populations in the Pacific Northwest may not be as important in the short term as making people aware of the status and providing federal protection for the populations. That the populations appear dangerously low should be sufficient to generate protection; discussions and research into the reasons should occur after protection. In our opinion, protection by the states of Washington, Oregon, and California has not been sufficient to improve population status.

The status of fishers in the northern and central Sierra Nevada is unknown but the absence of recent observations suggests they are declining or barely holding steady (Gibilisco 1994). Fisher populations in the northern Rocky Mountains of the United States do not appear to be in as critical condition as those in the Pacific Northwest. Although fishers have not recolonized all of their former range in this region, some healthy fisher populations exist. Fishers were never found much farther south than the Yellowstone region. If trapping seasons are regulated carefully in Montana to prevent overtrapping, fisher populations may slowly expand in Montana and Idaho. If fisher populations are limited by deep snow, however, fishers may never reach high densities in these mountain states.

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Chapter 4

Lynx

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INTRODUCTION

Natural History

Three species of wild cats (felids) occur in the temperate forests of North America: the cougar (*Fells concolor*), bobcat (*Lynx rufus*), and lynx (*Lynx canadensis*). The cougar is found in both temperate and tropical forests from the mountains of southern British Columbia to the southern tip of South America, whereas the bobcat and lynx are restricted to the temperate zone of North America. Bobcats are common throughout a variety of habitats in the conterminous United States, southernmost Canada, and northern Mexico. The lynx, in contrast, occurs primarily in the boreal forests of Alaska and Canada, but its range extends south into the northern portions of the western mountains, where environmental conditions at high elevations support boreal forest habitats similar to those found in northern regions.

The bobcat and lynx are both short-tailed cats, but the bobcat is smaller than the lynx and has relatively shorter legs and smaller paws. The lynx's short tail is completely tipped with black, whereas the bobcat's tail is generally longer and is barred with black only on the upper surface (Nowak and Paradiso 1983). The bobcat looks much like a house cat (*Fells catus*) in body form but is about two or three times larger. The lynx differs in body proportions, however, having relatively long legs and hind legs that are longer than the forelegs, giving it a stooped appearance (Quinn and Parker 1987).

The winter pelage of the lynx is dense and has a grizzled appearance with grayish-brown mixed with buff or pale brown fur on the back, and grayish-white or buff-white fur on the belly, legs, and feet. Its summer pelage is more reddish to gray-brown. Male lynx are slightly larger than females, with total length averaging 85 cm compared to 82 cm, and weight averaging 10 kg for males and 8.5 kg for females (Quinn and Parker 1987). Both sexes have prominent ear tufts and a flared facial ruff. The paws of the lynx have twice the surface area of those of the bobcat (Quinn and Parker 1987). The lynx's long legs and broad paws enable it to negotiate the deep snows of the boreal forests and effectively hunt its principal prey, the snowshoe hare (*Lepus americanus*). The bobcat, lacking these features, is largely restricted to habitats where deep snows do not accumulate (Koehler and Hornocker 1991). Despite physiological and behavioral differences that may permit lynx and bobcats to exploit different niches (Parker et al. 1983), lynx apparently do not compete well with bobcats (Parker et al. 1983; Turbak 1991). Thus, habitat alterations that favor a northward range expansion by bobcats may not bode well for lynx, particularly in suboptimal habitats.

The distribution and abundance of the lynx appears to be tied to that of the snowshoe hare. Both species are confined to northern forest environments (Hall 1981). Hares seek dense conifer thickets to feed on woody seedlings and saplings and to escape predators and extreme cold; lynx frequent these habitats in search of prey. When foraging, lynx select forested habitats where hares are plentiful and use this cover to stalk or wait for hares to appear. From the forested peninsulas of western Alaska to the eastern islands of Canada and in the mountains of the western United States, hares comprise 35-97% of the lynx diet (table 1). Although snowshoe hares are the primary food for lynx throughout its range, they also feed on mice, squirrels, grouse, and ptarmigan, especially during the summer months (McCord and Cardoza 1982).

Hares not only determine where lynx are found but also influence how many lynx may occupy an area. This is dramatically illustrated in Alaska and central Canada, where hare populations cycle in abundance at varying amplitudes, with population

Table I.--Percent occurrence of prey items in the winter diet of lynx determined from analysis of scats (ST) or digestive tracts (DT). Sample size in parentheses.

Season, location	Percent of sample				
	Hares	Tree squirrels	Mice	Ungulates	Grouse
Winter diets					
Alaska[1]					
(ST= 161)	64	10	9	5	7
Alberta[2]					
(DT = 879)	35-90	9-12	4-28	22-3	2-6
(ST = 260)	61	5	10	3	4
Alberta & NWT[3]					
(DT = 52)	79	2	10	6	10
Newfoundland[4]					
(ST,DT = 152)	85	-	5	>13	-
Nova Scotia[5]					
(DT = 75)	97	1	3	5	3
(ST = 55)	93	-	7	5	4
Summer diets					
Alaska[1]					
(ST = 42)	38	28	15	-	7
Alberta[2]					
(ST = 38)	71	2	87	5	5
Alberta & NWT[3]					
(DT = 23)	52	9	22	-	-
Newfoundland[4]					
(ST,DT = 92)	65	-	30	>3	-
Nova Scotia[5]					
(ST = 441)	70	4	4	9	1
Annual diets					
Washington[6]					
(ST = 29)	79	24	-	3	3

[1] *Staples and Bailey 1993, unpubl.*
[2] *Brand and Keith 1979, Brand et al. 1976.*
[3] *van Zyll de Jong 1966.*
[4] *Sounders 1963o.*
[5] *Parker et al. 1983.*
[6] *Koehler 1990.*

densities changing 2-200 fold within a 5-year period. As this phenomenon is repeated, periods of hare scarcity occur approximately every 10 years (Brand and Keith 1979). In areas where snowshoe hare populations exhibit this cycle, lynx also undergo dramatic population fluctuations. As part of a predator-prey oscillation, lynx populations lag several years behind hares, going from near extinction to densities of 10 to 20 lynx/100 km^2 during their population peaks (Bailey et al. 1986; Brand and Keith 1979; Parker et al. 1983). At the southern limits of its distribution, however, snowshoe hare populations do not undergo dramatic cycles due apparently to the presence of predators and competitors that do not occur in northern regions and to the patchiness of suitable habitat (Dolbeer and Clark 1975; Wolff 1980, 1982). Consequently, lynx populations appear also not to cycle in abundance at southern latitudes (Koehler 1990). In general, lynx and snowshoe hares in the western mountains of the United States exhibit life history characteristics similar to those occurring during hare population lows in the northern boreal forests (Brittell et al. 1989, unpubl.; Koehler 1990; Dolbeer and Clark 1975; Wolff 1980, 1982). This difference in the population dynamics of lynx and snowshoe hares in the southern portions of their ranges has strong implications for the management and conservation of lynx in the western mountains.

Several excellent literature reviews have recently been produced that describe lynx and snowshoe hare

biology in northern areas where populations are cyclic (Butts 1992, unpubl.; Washington Dept. of Wildlife 1993, unpubl.; Weaver 1993, unpubl.). The emphasis of this chapter, however, will be on the population dynamics and habitat relationships of lynx in either the western mountains or in northern boreal forests during times of low hare densities. This information provides the most meaningful conceptual framework for management and conservation of lynx in the western mountains.

During periods of hare and lynx abundance in northern regions, when competition for prey is keen and available territories are occupied or, during periods of prey scarcity after hare numbers have crashed, lynx may undergo dramatic movements in search of adequate prey (Poole 1993, unpubl.). During these times, lynx have been known to travel as far as 1,100 km (Mech 1980; Poole 1993, unpubl.; Slough and Mowat 1993, unpubl.) and are found in atypical habitats, such as agricultural areas or geographic areas far south of their normal range (Mech 1980). Although speculative, this process may be important for the persistence of lynx populations in marginally suitable habitats at the periphery of their range. In addition, these extensive movements presumably facilitate gene flow among populations, which may explain why the lynx appears to be genetically homogeneous throughout its range; all lynx populations, with the exception of those occurring in insular Newfoundland, are classified as a single subspecies (Hall 1981).

Current Management Status

As with most felids of the world, except for those that are classified as threatened or endangered with extinction, the lynx is listed on Appendix II of the Convention on International Trade of Endangered Species. This listing requires the exporting country to provide evidence that trade will not threaten or endanger the species and that items of trade, such as pelts, be regulated and monitored.

Lynx populations in Alaska and most of Canada are generally considered stable (table 2), although few reliable population estimates have been made (Anonymous 1986, unpubl.; Quinn and Parker 1987). Large populations are found in southern Quebec, northern British Columbia, Yukon, and Northwest Territories (IUCN, in press). In Canada, lynx are considered endangered only in New Brunswick; however, they are believed to have been extirpated from Prince Edward Island and mainland Nova Scotia. Lynx are considerably more rare in the conterminous United States. The largest populations in the United States outside of Alaska occur in the northern portions of Washington and Montana.

A petition was submitted to the U.S. Fish and Wildlife Service (USFWS) in August 1991 to list the lynx as endangered in the northern Cascade Range of Washington. In February 1992, the USFWS denied the petition because substantial scientific or comer-

Table 2.-Current management status of lynx in states and provinces of North America and lands of federal jurisdiction within the United States (Anonymous 1986, unpubl.; Butts 1992, unpubl.; IUCN, in press; Washington Dept. of Wildlife 1993, unpubl.).

Jurisdiction	Status or classification	Seasons or regulations
Alaska	Furbearer Fur animal	Hunting or trapping permit required, harvest limit 2, season 1 to 4.5 months,
Colorado	Endangered	
Idaho	Furbearer	Quota 3, December season, hunting or trapping permit required.
Maine	Protected	
Michigan	Protected	
Minnesota	Furbearer	Closed season since 1984.
Montana	Furbearer	Quota of 2, Season 1 Dec-15 Feb.
New Hampshire	Protected	
New York	Protected	
North Dakota	Furbearer	Closed season since 1981.
Oregon	Game Species	Closed season.
South Dakota	Nongame Monitor Species	
Utah	Threatened	
Vermont	Protected	
Washington	Threatened	
Wisconsin	Endangered	
Wyoming	Protected	
Alberta		Harvest seasons.
British Columbia		Harvest seasons.
Northwest Territories		Harvest seasons.
New Brunswick	Endangered	
Newfoundland		Harvest seasons.
Nova Scotia	Extirpated on peninsula	Closed since 1980.
Ontario		Harvest seasons.
Prince Edward Island	Endangered	
Quebec		Harvest seasons.
Saskatchewan		Harvest seasons.
Yukon		Harvest seasons.
USDA Forest Service	Sensitive	Region 1,2,4,6.

cial evidence was not available indicating that the lynx population in the north Cascades should be listed as endangered (Federal Register 1992). In April 1992, the USFWS agreed to reevaluate its 90-day finding on the petition in light of new information submitted by the petitioners. The USFWS found that there was no substantial new evidence indicating that the requested action was warranted and concluded that the north Cascades lynx population is not listable because it is not isolated from lynx populations elsewhere (Federal Register 1993). The USFWS also found, however, that a status review should be conducted throughout lynx range in the conterminous United States; this review is currently underway.

The lynx was classified as endangered in Colorado in 1973 (Halfpenny and Miller 1980, unpubl.) and Washington listed the lynx as threatened in October 1993 (Washington Dept. of Wildlife 1993, unpubl.). The lynx is protected or is considered to be a species of special concern in Wyoming and Utah, but it is still trapped during a restricted season in Idaho and Montana (table 2). The USDA Forest Service, which administers the majority of lands where lynx occur in the conterminous United States, considers the lynx to be a sensitive species in all Regions containing lynx populations (Regions 1, 2, 4, and 6; see Appendix C). This designation refers to species for which population viability is of concern as evidenced by significant current or predicted downward trends in population numbers, population density, or habitat capability.

Lynx are relatively common throughout forested areas of Alaska and most of Canada, although intensive trapping in the past has eliminated or temporarily reduced numbers in localized areas within that region (Bailey et al. 1986; Todd 1985). The conservation of lynx populations is of greatest concern in the western mountains of the conterminous United States at the southern periphery of the species' range. Because recruitment is low in this region and many lynx populations, especially those in Utah, Wyoming, and Colorado, are geographically isolated, trapping and forest management activities may pose significant threats to the persistence of these populations.

DISTRIBUTION, TAXONOMY, AND ZOOGEOGRAPHY

Distribution in North America

Lynx occupy regions in North America of arctic or boreal influence. They are restricted to forested habitats within this region and are found from western Alaska to the eastern edge of Newfoundland. The northern boundary of this range coincides with the northern extension of the boreal forests; lynx are absent north of the Ungava Peninsula in Quebec and in the northern regions of the Northwest Territories (Anonymous 1986, unpubl.). The lynx's historic range also included the northern portions of the conterminous United States in the Cascade Range of Washington and Oregon, south in the Rocky Mountains to Utah and Colorado, and east along the Canadian border to the Lake States (McCord and Cardoza 1982; Quinn and Parker 1987).

Except for the southern boundary of its range, the distribution of lynx in North America probably has not changed much during historical times (Quinn and Parker 1987). Destruction of forests for timber and incursions of agriculture and settlements, however, may have displaced lynx occurring in the Lake States (Jackson 1961) and southern regions of Manitoba to Alberta (Anonymous 1986, unpubl.; Quinn and Parker 1987). Lynx have probably been extirpated from Prince Edward Island and the mainland of Nova Scotia (Anonymous 1986, unpubl.), and their range appears to have retracted on Cape Breton Island .after the introduction of bobcats (Parker et al. 1983).

Taxonomy

The taxonomic status of the lynx is an issue of controversy among authorities. The debate concerns both the generic status of lynx throughout the world and the specific status of lynx in North America. It is unclear whether lynx throughout the world should be classified within a separate genus *Lynx*, or whether they should be placed within the more inclusive genus *Felis*. In either case, there is also confusion about whether the Canadian lynx should be considered a separate species from the Eurasian lynx. Thus, some authorities (McCord and Cardoza 1982; Tumlinson 1987) consider the Canadian lynx to belong to the Holarctic species *Felis lynx*. Others (Jones et al. 1992) agree that lynx represent a Holarctic species but consider lynx to be generically distinct from other cats and place the Canadian lynx within the species *Lynx lynx*. Others (Hall 1981; Wozencraft 1989, 1993), however, believe that Eurasian and Canadian lynx represent distinct species and place the Canadian lynx in the species *Lynx canadensis*.

Lynx and bobcat are believed to have evolved from Eurasian lynx that immigrated to North America

from Asia via the Bering land bridge during the Pleistocene (Quinn and Parker 1987; Tumlinson 1987). It is speculated that the bobcat and the Canadian lynx represent the descendants of two separate colonizations of North America by the Eurasian lynx. The first immigrants became established in the southern portions of the continent about 20,000 years ago, when glaciers covered the northern regions. These populations, that were isolated in ice-free areas in the southern portions of the continent, evolved into the bobcat. Some time later, the North American continent was invaded by Eurasian lynx a second time. These populations established themselves in northern boreal forests in areas that were occupied previously by glaciers, and evolved into the Canadian lynx (Quinn and Parker 1987).

Zoogeography of Lynx in the Western Mountains

The boreal forests of Canada and Alaska are the primary habitat of lynx in North America. Populations occurring in the western mountains of the conterminous United States occupy peninsular extensions of this distribution. Lynx distribution at southern latitudes represents the occupation of marginally suitable habitat that decreases in quality and availability as one moves southward. Ecoprovinces where lynx populations occur in the western mountains include the Thompson-Okanogan Highlands of northeastern Washington, the Shining Mountains of northern Idaho and northwestern Montana, the Northern Rocky Mountain Forest of southwestern Montana and northwestern Wyoming, and the Colorado Rocky Mountains of west-central Colorado (see Appendices A and B). A brief review of the historical zoogeography and current population status and ecology of lynx and snowshoe hares in the western mountains will illustrate the marginal nature of boreal habitats in that region.

Lynx have apparently never occupied the Sierra Nevada of California in historic times (Grinnell et al. 1937; Ingles 1965). Although the lynx has been found in Oregon, historical records indicate that it has always been rare; only a few specimen records are known from high elevations of the Cascade Range and the Wallowa Mountains in the northeast (Bailey 1936). A lynx shot in northeastern Oregon in 1964 was the first record of a lynx being taken in Oregon since 1935 (Coggins 1969). Oregon clearly represents the southern margin of suitable lynx habitat along the Pacific Coast. Lynx are now considered to be extirpated from the state (Ingles 1965; McCord and Cardoza 1982), although several sightings have been reported recently (Zielinski, pers. comm.). Apparently, populations have always been so low in Oregon that they were unable to persist with the onset of human settlement of that region. The lynx still occurs in Washington, but its range has retracted northward. Taylor and Shaw (1927) reported the lynx to be a component of the fauna occurring in the higher elevations of Mount Rainier National Park in the central Washington Cascades, and Dalquest (1948) showed its range extending south in the Cascades to near the Oregon border on Mount Adams, and in the Blue Mountains in the southeastern corner of the state; there are no historic records of lynx in either the Olympic Mountains or Coast Range of Washington. A current description of lynx distribution in Washington (Washington Dept. of Wildlife 1993, unpubl.) indicates that lynx are now restricted to the northeastern Cascade Range and several isolated areas in the Okanogan Highlands of northeastern Washington. The Okanogan population was studied with radiotelemetry in the 1980's (Brittell et al. 1989, unpubl.; Koehler 1990) and most of the information available on the ecology, population dynamics, and management of lynx in the western mountains of the United States comes from these studies.

This pattern of decreasing habitat suitability with decreasing latitude is also evident in the Rocky Mountains. Lynx populations are also present in northern Idaho and western Montana. Historical records are relatively numerous in the panhandle of Idaho; Davis (1939) reported lynx occurring in the mountainous regions north and east of the Snake River in Idaho, and Rust (1946) claimed that they were fairly well distributed in wooded areas of the northern counties with 25 or 30 lynx being taken annually by trappers and hunters. Historical reports from western Montana also indicate that the lynx was fairly numerous in recent times. Bailey (1918) lists the lynx as being more or less common throughout Glacier National Park, and the Montana Fish and Game reports that from 1959-1967, a total of 990 lynx were taken by trappers statewide (Hoffman et al. 1969). According to Hoffman et al. (1969), lynx are most common in the northwestern areas of the state, and they decrease in abundance south and east. Populations in western Montana are large enough for scientific study; two radiotelemetry studies of

lynx movements in western Montana were conducted in the early 1980's (Brainerd 1985; Smith 1984).

Although early trappers had apparently reported taking lynx from northern Nevada (Bailey 1936), Hall (1946) includes the lynx on a list of hypothetical species for Nevada based on a lack of museum specimens. Further investigation by Schantz (1947), however, revealed the existence of a single specimen of lynx taken from north-central Nevada in 1916. Records of lynx are scarce in Wyoming, Utah, and Colorado. A review of existing records of lynx in Wyoming by Long (1965) shows that 15 museum specimens exist, and all are from the northwestern corner of the state. According to Long (1965) the lynx was "confined to high, inaccessible (to man) ranges of northwestern Wyoming, if not extirpated at the time of this writing." Later authors (Clark and Stromberg 1987; Clark et al. 1989) agree that the lynx remains extremely rare in Wyoming.

Reports by trappers in 1915 and 1916 (Barnes 1927) suggest that lynx were relatively common in Utah at that time; however, Durrant (1952) questions the validity of these reports. He believes that many of these records are actually of bobcats because the feet and tail are often removed from pelts, and also because large bobcats are commonly referred to as lynx cats in the fur trade. Durrant (1952) reports that only two lynx from Utah exist in museum collections, and he is of the opinion that "if *L. c. canadensis* occurs at all in Utah at present, there are only a few animals in the Uinta Mountains" in north-central Utah. Although seven lynx specimens were collected from the Uinta Mountains in Utah from 1957-1972, since that time only sightings and tracks have been reported (McKay 1991, unpubl.).

Nine museum specimens of lynx exist from eight counties in Colorado (Halfpenny and Miller 1980, unpubl.), but it is generally agreed that lynx were never numerous in the state and are presently extremely rare (Lechleitner 1969; Halfpenny and Miller 1980, unpubl.). Four of these specimens were collected from 1969-1972, and all were from a relatively small area in the west-central portion of the state (Halfpenny and Miller 1980, unpubl.). Records from this state represent the southernmost extension of current lynx distribution in North America.

Existing records clearly show that lynx are rare at the southernmost extensions of its range in Wyoming, Utah, and Colorado, both historically and at present, and that any populations that occur in this area are disjunct and isolated in distribution. It seems doubtful, therefore, that gene flow is occurring among these populations. Because boreal habitat is found at higher and higher elevations as one moves southward in the western mountains, suitable habitat for lynx eventually becomes scattered on isolated mountain peaks (Findley and Anderson 1956). Museum records of lynx in Wyoming, Utah, and Colorado overlap precisely with the range of boreal forest habitat depicted by Findley and Anderson (1956). Given the rarity of records and the dispersal capabilities of lynx, it is possible that existing records represent short-term residents or individuals wandering and dispersing, rather than reproductively stable populations; viable lynx populations may never have occurred in historic times in the southern Rocky Mountains. Thus, lynx conservation efforts may best be directed at populations occurring in northeastern Washington, northern Idaho, and western Montana.

Because they are contiguous with lynx populations that undergo periodic dramatic increases in numbers, populations near the Canadian border may have benefitted from periodic incursions of lynx as populations peaked in northern latitudes (Hoffman et al. 1969; Mech 1980; Quinn and Parker 1987). For example, there were dramatic increases in lynx harvests in western Montana and the northern Great Plains in 1962-1963 and 1971-1972 (Adams 1963; Hoffman et al. 1969; Mech 1973). However, after a population irruption of lynx in Minnesota following a cyclic high in Canada in 1972, trappers reported capturing 215 lynx in 1972, 691 in 1973, 88 in 1974, and 0 in 1975 (Mech 1980). Mech (1980) also showed that immigrating lynx occupied very large home ranges, exhibited little reproductive productivity, and were susceptible to human-caused mortality. Thus, immigration of lynx into marginal habitats during population highs in the north may ultimately have little effect on their population persistence at lower latitudes.

Management Considerations

1. Because of the peninsular and disjunct distribution of suitable lynx habitat in the western mountains of the conterminous United States, populations in that region are likely to be of greatest conservation concern.

2. Both historical and recent lynx records are scarce from the western mountains, which makes identifying range reductions and determining the historical distribution of reproductively stable populations in that region difficult, if not impossible.

Research Needs

1. Reliable information on the current distribution and abundance of lynx populations throughout the western United States is urgently needed.

POPULATION ECOLOGY

Population Dynamics of Snowshoe Hares and Lynx in the Western Mountains

The 10-year cycle of dramatic increases in population densities for both snowshoe hares and lynx in the boreal forests of Canada and Alaska is well-known (Keith 1963; Brand and Keith 1979; Brand et al. 1976; Nellis et al. 1972; and others). Although this phenomenon is of critical importance for the conservation and management of lynx populations in northern boreal, forests, neither lynx (Brittell et al. 1989, unpubl.; Koehler 1990) nor snowshoe hare (Chitty 1950; Dolbeer and Clark 1975; Wolff 1980; Koehler 1990) populations in the western mountains of the United States exhibit such cycles. It appears, rather, that both species occur in that region at relatively stable densities comparable to those occurring during population lows in the northern boreal forests (Brittell et al. 1989, unpubl.; Koehler 1990; Wolff 1980, 1982).

A compelling hypothesis has recently been proposed by Wolff (1982) to explain this latitudinal variation in the population dynamics of hares and lynx. Wolff speculates that the presence of additional predators and competitors of hares at lower latitudes largely accounts for this pattern. Apparently, during hare population lows in Alaska, hares occupy less than 10% of suitable hare habitat, which appears to be comparable to the normal dispersion of hares in the western mountains. As population density increases in northern regions, hares begin dispersing into suboptimal and marginal habitats. When predator populations have crashed and competitors are few, hares moving into such habitats are able to establish themselves and reproduce, and the population slowly builds again in numbers. In contrast, hares dispersing into low-quality habitat in Colorado suffer increased mortality from predation and are not able to establish themselves in such habitats (Dolbeer and Clark 1975). The reproductive rates of hares in Colorado did not differ significantly from those in northern regions, indicating that limitations in the intrinsic rate of increase do not explain the latitudinal gradient in population cycles (Dolbeer and Clark 1975). Rather, the apparent lack of hare population cycles in the western mountains is best explained as resulting from the presence of more stable populations of predators, lower-quality suboptimal habitats, and, possibly, from the presence of fewer competitors at southern latitudes. In addition, a regional mosaic of early successional habitats created by frequent large-scale wildfires in northern forest ecosystems may contribute to higher quality lynx and hare habitats in that region (T. Bailey, pers. comm.).

The major predators of hares in the north are the lynx, goshawk (*Accipiter gentilis*), red fox (*Vulpes vulpes*), and great-horned owl (*Bubo virginianus*). In that region, lynx, goshawk, and great-horned owl are obligate, migratory predators that all exhibit a delayed density-dependent cycle with snowshoe hares, resulting in a relaxation of predation pressure after snowshoe hare populations have crashed. In contrast, the major predators of snowshoe hares in the western mountains are the coyote (*Canis latrans*), bobcat, red fox, and several species of hawks and owls. These predators are facultative and resident, and their populations do not cycle in response to hare numbers. The presence of predators at stable densities prevents snowshoe hares from becoming established in suboptimal habitats. Boreal forest habitat in northern regions tends to be relatively continuous in distribution. The insular nature of preferred habitats in the south, however, whereby adjacent habitats can be of very low quality, may hinder the occupation of suboptimal habitats by snowshoe hares. No other species of leporid occupies the northern boreal forests; thus, the presence of potential competitors such as jackrabbits (*Lepus* spp.) and cottontails (*Sylvilagus* spp.) in the western mountains may also limit snowshoe hare populations.

Reproductive Biology

Lynx have a high potential for population growth but, as with other life history parameters, recruitment is influenced by the abundance of its principal prey, the snowshoe hare (Bailey et al. 1986; Brand and Keith 1979; Brand et al. 1976; Nellis et al. 1972; O'Conner 1986; Parker et al. 1983; Slough and Mowat 1993, unpubl.). Recruitment is high during periods of hare abundance primarily because of increased kitten survival. However, periods of high hare numbers are also accompanied by increased reproductive rates for yearlings and increased litter sizes among females in all age classes (Brand and Keith 1979; Brand et al. 1976; O'Conner 1986; Parker et al. 1983).

From examination of necropsied carcasses from Alaska, O'Conner (1986) found lynx to ovulate from late March to early April and give birth in late May after a gestation period of 60-65 days. This breeding schedule has also been reported for Ontario (Quinn and Thompson 1987), Alberta (Nellis et al. 1972) and Newfoundland (Saunders 1964). Kittens observed in north-central Washington in early July (Koehler 1990, unpubl. data) appeared to have been born in late May or early June, suggesting that conception occurs in March and April at southern latitudes as well. In Alaska, the mean number of corpora lutea and placental scars, the age of first breeding, the proportion of females breeding, the proportion of kittens breeding, and the percentage of juveniles present in the population all reached highest levels the first spring after hare numbers peaked (O'Conner 1986). This time lag may differ in other regions depending on the density of predators other than lynx, weather factors, and availability of alternate prey (O'Conner 1986).

Brand et al. (1976) found that females were capable of becoming pregnant at 10 months of age under optimal conditions, based on the presence of corpora lutea, but Parker et al. (1983) concluded that most females reach reproductive maturity at 22 months. Age of first ovulation can be influenced by hare abundance, however; 61-99% of lynx ovulate as kittens during periods of hare abundance compared to only 10-49% as hare numbers decrease (O'Conner 1986, van Zyll de Jong 1963, Brand et al. 1976, Brand and Keith 1979). Quinn and Thompson (1987) found that 96% of yearlings, 99% of 2-year-olds, and 100% of females >3 years old ovulated during a period of hare abundance in Ontario. O'Conner (1986) also demonstrated a difference in ovulation rates between periods of hare scarcity and abundance. During times of hare abundance, counts of corpora lutea averaged 6.2 ± 0.3 (95% CI) to 6.4 ± 1.1 for yearlings (indicating they ovulated as kittens) and 16.5 ± 1.3 to 15.4 ± 2.3 for adults, compared to periods of hare scarcity when counts were 0.5 ± 0.7 for yearlings and 8.6 ± 1.3 for adults.

Counts of placental scars have been used to estimate pregnancy rates and *in utero* litter sizes, although such counts may not accurately reflect actual litter size because some implanted embryos may not survive (Quinn and Thompson 1987). Pregnancy rates range from 33-79% for yearlings and 73-92% for adults during periods of hare abundance, compared to rates of only 0-10% for yearlings and 33-64% for adult females when hares were scarce (Brand and Keith 1979; O'Conner 1986; Quinn and Thompson 1987). During a period of hare abundance, Quinn and Thompson (1987) found that although 96% of yearlings ovulated, only 33% became pregnant, whereas 80% of 2-year-olds and 92% of females >3 years old became pregnant. Brainerd (1985) examined 20 female carcasses from western Montana and found pregnancy rates of 44.4% for juveniles and 100% for adults. Among lynx that had colonized areas of low prey density in Minnesota, only 1 of 14 live-captured females showed signs of nursing and only 2 of 22 female carcasses examined showed evidence of implantation (Mech 1980). The number of placental scars averaged 3.5-3.9 for yearlings and 4.4-4.8 for adults during periods of hare abundance, which decreased significantly to 0.2 for yearlings and 1.4-3.4 for adults when hares were scarce (Brand and Keith 1979; O'Conner 1986; Parker et al. 1983; Quinn and Thompson 1987). Average litter size (based on placental scars) in western Montana was 2.75, with a range of 1-5; litter size for yearlings was 1.75 and for adults, 3.25 (Brainerd 1985).

During hare population declines, there is increased kitten mortality prior to winter. Brand et al. (1976) found no kittens present on their Alberta study area during a low in hare numbers. Kitten production and survival in north-central Washington during 5 1/2 years of a 7-year period (1980-1983, 1985-1987) was comparable to a 5-year period of low productivity measured at northern latitudes when hares were scarce (Brittell et al. 1989, unpubl.; Koehler 1990; Brand et al. 1976).

In Alberta, recruitment of kittens to the winter population decreased dramatically 2 years after the peak, and was near zero for 3-4 years during periods of hare scarcity (Brand and Keith 1979). No litters were produced during 5 winters when hare densities were lower than 1.4 hares/ha, and mean litter size increased from 1.3-3.5 as hare density increased from 1.8-5 hares/ha (Brand et al. 1976). In north-central Washington where hare numbers were believed to be low, Koehler (1990) found only 1 kitten surviving to the winter from 8 kittens present among 3 litters in July, indicating that kitten mortality is high during the snow-free season. A disparity in the ratio of females with corpora lutea compared to those observed nursing from August to October, and the few kittens present in fall harvest figures, led Nellis et al. (1972) and Parker et al. (1983) to speculate that several factors result in lower reproductive rates during periods of hare scarcity, including preimplantation

losses, intrauterine losses, and mortality of kittens during summer.

Mortality

As with reproductive parameters, mortality is also influenced by the relative abundance of hares. Although data are scarce, natural mortality rates for adult lynx average ≤ 27% per year (Koehler 1990; Slough and Mowat 1993, unpubl.). Bailey et al. (1986) observed no mortality from predation or disease between 1977 and 1984 on their study area in Alaska. In the Yukon, Ward and Krebs (1985) found only 1 of 11 radio-collared animals dying from natural causes. Brand and Keith (1979) calculated natural mortality rates from May to November in Alberta of 34-68% during a snowshoe hare decline. In the Northwest Territories, annual mortality for radio-collared lynx increased from 0.10-0.79 as hares declined (Poole 1993, unpubl.). Although starvation appears to be the most significant cause of natural mortality, predation also occurs (Koehler 1990; Koehler et al. 1979; Poole 1993, unpubl.).

During periods of decreasing hare numbers, mortality rates for kittens may be three times that for adults (Brand and Keith 1979). The cause of postpartum mortality of kittens is most likely related to starvation, as females are more likely to feed themselves first (Brand and Keith 1979). Thus, it appears there may be a minimum density of hares at which females are no longer able to successfully rear kittens (Nellis et al. 1972). Koehler (1990) observed a kitten mortality rate of 88% during summer-fall seasons for 8 kittens from 3 litters in Washington, which is similar to mortality rates of 65-95% for kittens in Alberta during a 3-year period of hare scarcity (Brand and Keith 1979). Mortality for kittens of juvenile females is higher (80-100%) than that for kittens of older females (30-95%), indicating that juveniles contribute little to recruitment (Slough and Mowat 1993, unpubl.).

Trapping can be a significant source of mortality for lynx (Bailey et al 1986; Carbyn and Patriquin 1983; Mech 1980; Nellis et al. 1972; Parker et al. 1983; Ward and Krebs 1985). During a period of high recruitment in Ontario, Quinn and Thompson (1987) estimated overall trap mortality for lynx at 38%. Where exploitation is intense and recruitment is low, trapping can significantly depress lynx populations. In the intensively trapped Kenai National Wildlife Refuge in Alaska, Bailey et al. (1986) found that trapping accounted for 44-86% of annual mortality and estimated that trappers may have removed as much as 80% of the lynx population in their study area. Parker et al. (1983) estimated that trappers removed 65% of their study population in Nova Scotia. Among 14 radio-collared animals in Minnesota, at least 7 were killed by humans (Mech 1980), and all 5 study animals in Manitoba and 8 of 11 in the Yukon were taken by trappers (Carbyn and Patriquin 1983; Ward and Krebs 1985). On the Kenai Peninsula, juveniles were 5 times more vulnerable to trapping than adults, a phenomenon that may be associated with family cohesiveness, since several juvenile siblings can easily be trapped from a small area (Bailey et al. 1986).

Trapping females that are accompanied by kittens often results in the death of those kittens (Bailey et al. 1986; Carbyn and Patriquin 1983; Parker et al. 1983). Bailey et al. (1986) reported that 2 of 3 kittens starved to death after their mothers were trapped. Apparently kittens are unable to obtain sufficient prey by themselves during the winter (Bailey et al. 1986). Yearlings also appear to be dependent upon their mothers for survival. Parker et al. (1983) observed an increase in numbers of yearlings trapped as the harvest season progressed, presumably because more yearlings were orphaned. In addition, kittens of yearling females have higher mortality rates (80-100%) than kittens from adult females (30-95%) (Slough and Mowat 1993, unpubl.).

Emigrating or nomadic lynx can suffer high trapping mortality. In the Yukon, during a period of low hare numbers, Ward and Krebs (1985) reported that all radio-collared lynx that emigrated from their study area were subsequently trapped. Slough and Mowat (1993, unpubl.) found that 10-20% of lynx that emigrated from or that occupied areas peripheral to their untrapped study area were harvested by trappers. Fur harvest returns for lynx also indicate a differential rate of mortality among the sexes, whereby males are more vulnerable than females to trapping mortality (Mech 1980; Parker et al. 1983; Quinn and Thompson 1987), presumably because of their greater mobility and larger home ranges. This pattern has been demonstrated for other furbearers, as well (Buskirk and Lindstedt 1989). Assuming an even sex ratio at birth, Quinn and Thompson (1987) showed from fur harvest records that the annual rate of trap mortality for males was 0.46 ± 0.26 (90% CI) compared to 0.28 ± 0.17 for females, and that increased male vulnerability begins at the age of 1.5 years. Bailey et al. (1986) also found males to be twice as vulnerable to trap mortality as females.

Trapping mortality appears to be additive, since most natural mortality occurs during summer

months prior to the winter trapping season. In their Alberta study area, where lynx trapping did not occur, Brand and Keith (1979) observed no change in the population over the winter, although populations declined elsewhere where trapping occurred. The importance of trapping as a source of mortality is correlated to the price of lynx furs (Todd 1985). Brand and Keith (1979) estimated that only 10% of the fall population was trapped when pelt prices averaged $44/pelt, whereas 17-29% were trapped when prices increased to $101 /pelt.

Age and Sex Structure

Fur harvest data can provide an indication of the direction and amplitude of population changes (O'Conner 1986), although caution must be applied when using these data to interpret population parameters. For example, Brand and Keith (1979) found only a 4.3-fold increase in lynx numbers on their Alberta study area when harvest data for the Province indicated a 20-fold increase. Caution should also be applied when using harvest statistics to estimate population sex ratios. In Ontario, 58% of trapped lynx were males (Quinn and Thompson 1987), whereas in Alberta, 71% were males (Brand and Keith 1979).

As the density of hares declines, the proportion of kittens in harvest samples decreases. O'Conner (1986) examined trapper-killed carcasses and found that during periods of hare abundance in 1963-1964 (N=745) and 1970-1971 (N=114), 40% and 32% of lynx trapped were kittens and 40% and 55% were yearlings, respectively. Harvest percentages dropped to 0-3% for kittens and 8-17% for yearlings, however, when hare numbers were low. In Alberta, as hare numbers dropped, the proportion of kittens went from 31-7% (Brand and Keith 1979), and Parker et al. (1983) documented a decline from 29-2% for kittens and 52-39% for yearlings during a hare decline in Nova Scotia.

Brand and Keith (1979) found only 1 kitten among 518 lynx trapped during a 3-year period of hare scarcity in Alberta. During the first year of decline in hare numbers, yearling and 2-year-old lynx comprised 85% of the harvest; during the second year, 2- and 3-year-olds made up 78% of the harvest; and by the third year, the harvest contained 78% 3- and 4-year-olds. As hare numbers declined dramatically from 1971-1976, the mean age of trapped lynx rose from 1.6-3.6 years (Brand and Keith 1979). At southern latitudes, where hare densities are typically low (Dolbeer and Clark 1975), older age individuals appear to predominate in lynx populations. Brittell et al. (1989, unpubl.) reported an average age of 4.5 years for 14 lynx harvested in Washington from 1976-1981.

Density

In northern regions, where hare populations cycle, lynx populations respond with a 1- to 2-year lag (Breitenmoser et al. 1993; Brand et al. 1976; O'Conner 1986). Increases in prey numbers result in higher densities of lynx from increased reproduction and decreased mortality. Although social intolerance may separate lynx in time and space (Brand et al. 1976), it does not appear to be a major factor limiting their densities (Breitenmoser et al. 1993; Bergerud 1971).

During periods of hare scarcity, lynx congregate around pockets of hare activity, which may result in inflated density estimates for lynx if extrapolated to other habitats (Bergerud 1971; Carbyn and Patriquin 1983; Todd 1985; Ward and Krebs 1985). On the Kenai National Wildlife Refuge, where overall lynx densities were 1/100 km^2, densities were 2.3/100 km^2 in an area that burned in 1947 where hare numbers were high (Bailey et al. 1986). Carbyn and Patriquin (1983) reported trappers removing 16 lynx from 3 km^2 of high-quality habitat during mid-winter. Such focal areas of lynx activity and localized densities may lead to erroneous population estimates when based on trapper interviews or fur harvest returns.

Snow-tracking studies in Alberta showed that lynx densities increased from 2.1-7.5/100 km^2 as hare numbers increased (Nellis et al. 1972). In the same study area, later workers (Brand and Keith 1979; Brand et al. 1976) observed a 4.3-fold change in lynx densities from 1966-1972, with the highest density of lynx occurring 1 year after the peak in hare numbers. Bergerud (1971) reported a lynx density of 7.7/ 100 km^2 on caribou (*Rangifer* spp.) calving grounds during June. In Alaska, Bailey et al. (1986) estimated that lynx trappers removed 10-17/ 100 km^2, suggesting that peak densities may have been greater than 20/ 100 km^2, a value equivalent to those reported on Cape Breton Island in Nova Scotia (Parker et al. 1983). Using radiotelemetry and snow-tracking to study lynx in Washington, Koehler (1990) estimated lynx densities of 2.3 adults/100 km^2 and 2.6 adults and kittens/ 100 km^2. Radiotelemetry studies also document changing lynx densities in response to changing hare numbers. In the Yukon, Slough and Mowat (1993, unpubl.) found that densities increased from 2.8/100 km^2 in 1987 to 37.2/100 km^2 in 1991 as hare

numbers increased, and then decreased to < 5/100 km^2 as hare numbers declined. Poole (1993, unpubl.) observed decreases in lynx densities from 35-2/100 km^2 in the Northwest Territories during the same period.

Changes in lynx densities may also be a function of intensity of exploitation. Densities were only 1/100 km^2 on the Kenai National Wildlife Refuge where populations were depleted from heavy trapping pressure (Bailey et al. 1986). After trapping was closed on the refuge, lynx densities increased 4-fold (1.6-6.8/100 km^2) during a period when hare densities were relatively stable (Kesterson 1988). During hare population declines, lynx become increasingly vulnerable to trappers as they expand their movements in search of alternate sources of prey (Brand and Keith 1979).

Management Considerations

1. The lack of dramatic fluctuations in lynx and snowshoe hare populations at southern latitudes will require management approaches that are different from those applied in northern boreal forests where populations are cyclic.

2. In the western mountains, the management of habitat for snowshoe hares is likely to be an important component of lynx conservation efforts due to the relatively low hare densities typical of boreal habitats in the western mountains, and because of the importance of hare availability for successful reproduction.

3. Due to its additive nature, trapping mortality can have significant short-term effects on lynx populations in the western mountains.

Research Needs

1. Implement monitoring and intensive research on lynx and snowshoe hare populations in the western mountains to determine the nature of their population dynamics and to understand why they do not exhibit dramatic fluctuations in numbers over time.

2. Where lynx are harvested in the western mountains, carcasses should be collected and age, sex, and reproductive data gathered.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

Foraging Ecology

Lynx occur in habitats where snowshoe hares are most abundant (Bailey et al. 1986; Bergerud 1971; Koehler 1990; Koehler et al. 1979; Parker et al. 1983; Ward and Krebs 1985). During periods of hare scarcity, lynx concentrate their activities in pockets of hare abundance (Bergerud 1971; Todd 1985; Ward and Krebs 1985), which are typically dense, brushy sites where hares seek refuge (Wolff 1980). Carbyn and Patriquin (1983) reported 16 lynx being trapped in an area 3 km^2 in extent.

Lynx apparently invest a great deal in learning to hunt, since kittens typically remain with their mother until they are 9-10 months of age (Bailey et al. 1986; Brand et al. 1976; Carbyn and Patriquin 1983; Koehler 1990; Koehler et al. 1979; Parker et al. 1983; Saunders 1963b). Their proficiency at hunting during their first 2 years is critical. When female lynx with kittens are trapped, the kittens are particularly vulnerable to starvation (Carbyn and Patriquin 1983).

When lynx are traveling, most of the time they are searching for food (Brand et al. 1976). Saunders (1963b) reported lynx to be most active from evening until early morning, although Parker et al. (1983) found that radio-collared lynx traveled during both day and night. The distance traveled during hunts, as determined by distances traveled between daytime beds, can vary from 8.8 km when hares are scarce to 4.7 km when hares are plentiful (Brand et al. 1976; Nellis and Keith 1968). Ward and Krebs (1985), however, found no significant difference in distances traveled per day until hare densities dropped below 1.0/ha. Parker et al. (1983) calculated daily cruising distances of 6.5-8.8 km in winter and 7.3-10.1 km during summer in Nova Scotia. In north-central Washington, females foraged up to 6-7 km from their den sites (Koehler 1990).

Cover is important for lynx to stalk prey. From snow-tracking, Brand et al. (1976) determined that lynx encountered and captured hares by following well-used hare runways, concentrating their movements in small areas of hare activity, or using short term "waiting-beds" (typically depressions in the snow) that were usually located near areas of hare activity. When numbers were declining, Brand et al. (1976) found lynx using waiting beds as a hunting strategy more frequently, and Saunders (1963b) reported that this strategy accounted for 61% of hares killed by lynx.

Prey Requirements and Hunting Success

Lynx are specialized predators of snowshoe hares, but they also forage opportunistically, preying on a variety of species as availability of resources change.

Most snow-tracking studies show the importance of hares to the lynx diet, even when hares are scarce and capture rates decrease (table 1). In Nova Scotia, Parker et al. (1983) found that 198 of 200 chases and 34 of 36 kills were of snowshoe hares, whereas in the Yukon, lynx were successful at capturing hares on 32 of 52 occasions (Murray and Boutin 1991). Among 361 attempts to kill prey in central Alberta, 73% were hares and 15% were ruffed grouse (*Bonasa umbellus*) (Brand et al. 1976). Hunting success did not differ among years as hare densities varied, averaging 24% during winters when hares were abundant, and 24-36% when hare numbers were low; capture rates for tree squirrels, however, varied from 0-67% (Brand et al. 1976; Nellis and Keith 1968). Snow-tracking lynx for 20.5 km in north-central Washington, Koehler (1990) detected 2 captures of hares in 6 attempts, and 2 unsuccessful attempts to capture red squirrels. Nellis and Keith (1968) believed that success in capturing hares was a function of snow conditions, experience, and familiarity with the area. Hunting success has also been shown to increase from 14-55% as the size of groups (usually a female and her kittens) increases from 1 to 4 (Parker et al. 1983).

Snow-tracking lynx in Alberta for 416 km, Nellis and Keith (1968) found lynx made 0.42 kills per day, less than half that reported by Parker et al. (1983) for lynx in Nova Scotia. Nellis et al. (1972) calculated a consumption rate of 593 g/day, which is similar to the 600 g/day calculated by Saunders (1963a). During a decline in hare numbers, the mean daily consumption rate of individual lynx may decrease by 37% (Brand et al. 1976). Nellis et al. (1972) found that a captive juvenile required about 370 gm/day of hares, tree squirrels, and birds to increase its body weight from 4.9 to 5.6 kg. This captive juvenile was smaller than recaptured wild littermates, suggesting that wild juveniles may require at least 400 g/ day to meet requirements for growth. Because the biomass of a grouse is equal to 0.5 hares and that of a tree squirrel to 0.2 hares (Nellis and Keith 1968), a shift to alternate food sources as hare populations decline may not compensate for the decrease in biomass of hares killed.

Lynx will occasionally prey on ungulates (Bergerud 1971; Koehler 1990; Stephenson et al. 1991), but the importance of ungulates in the diet appears to be insignificant. Bergerud (1971) found caribou calves to be more vulnerable to lynx predation during July and August when newborn calves are led by cows from open habitats to forested sites. Of 33 lynx scats collected on calving grounds, 13 contained caribou hair (Bergerud 1971). Saunders (1963a) and Bailey (pers. comm.) observed lynx scavenging moose (*Alces alces*) carcasses, and remains of deer (*Odocoileus* spp.) were infrequently found in lynx scats in Washington (Koehler 1990) and Nova Scotia (Parker et al. 1983). Whether the presence of deer hair in scats was from predation or scavenging is unknown.

Temporal and Spatial Variations in Diet

Studies in Alberta (Brand et al. 1976; Brand and Keith 1979; Nellis and Keith 1968, Nellis et al. 1972) have shown that although snowshoe hares make up the greatest biomass of prey consumed throughout the year, lynx use alternate prey during periods of hare scarcity and during the summer and fall seasons. Staples and Bailey (1993, unpubl.) and Saunders (1963a) also found a greater incidence of voles in lynx diets during summer (15-30%) than in winter (5-9%). Brand et al. (1976) reported that snowshoe hares represented only 27 of 71 food items during the summer, compared to 112 of 140 items in winter. In contrast, mice and voles represented 33 of 71 food items during summer, but only 22 of 140 during winter. Despite increased consumption of mice and voles during summer and fall, however, hares still comprised 91% of biomass consumed.

Brand and Keith (1979) observed a decline from 90 to 35% in the frequency of occurrence of hare remains in the diet as hares became scarce. However, the percent biomass of hares remained high, comprising 97% of the total biomass consumed when hares were abundant, and 65% when hares were scarce. During a decline in hare numbers, the frequency of voles and mice shifted from 4 to 28% of the diet and occurrence of tree squirrels increased from 9 to 12%. However, the percent biomass consumed of these species did not change much during the hare decline, remaining 3% for squirrels and 1% for mice and voles. In the only food habits study of lynx conducted in the western mountains, Koehler (1990) found that tree squirrels represented 24% of the food items found in 29 scats in his study area in north-central Washington; remains of tree squirrels were also found at den sites. Staples and Bailey (1993, unpubl.) found a similarly high percentage of squirrels in the diet of lynx in Alaska (28%) during a hare population low (table 1), providing additional evidence that lynx ecology in the western mountains is similar to that occurring in northern latitudes during lows in the snowshoe hare cycle.

Management Considerations

1. In the western mountains, prey species other than snowshoe hares, including tree squirrels, voles, and mice, appear to provide important alternate food sources for lynx.

Research Needs

1. Intensive studies of the food habits of lynx during all seasons of the year in the western mountains are urgently needed.

2. Determine the composition and structure of habitats in the western mountains that provide both sufficient food and cover for hares and adequate stalking cover for lynx.

HABITAT RELATIONSHIPS

Components of Lynx Habitat

From the coast of western Alaska to the eastern islands of Canada and the mountains of the western United States, the distribution of lynx is tied to boreal forests. Lynx occupy habitats at 122 m elevation dominated with white (*Picea glauca*) and black spruce (*P. mariana*), paper birch (*Betula papyrifera*), willow (*Salix* spp.), and quaking aspen (*Populus tremuloides*) on the Kenai Peninsula of Alaska (Bailey et al. 1986); white spruce-dominated forests in southwestern Yukon (Ward and Krebs 1985); aspen, poplar (*P. balsami fera*), and spruce stands in central Alberta (Brand et al. 1976); aspen forests in Manitoba (Carbyn and Patriquin 1983); balsam fir (*A. balsamea*), white spruce, black spruce, and paper birch forests to 390 m elevation on Cape Breton Island, Nova Scotia (Parker et al. 1983); jack pine (*Pinus banksiana*), balsam fir, black spruce, aspen, and paper birch forests in northern Minnesota (Mech 1980); Engelmann spruce (*P. engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*P. contorta*), and aspen forests above 1,463 m in north-central Washington (Koehler 1990); and similar forest communities in western Montana (Koehler et al. 1979). They occur in the Rocky Mountains above 1,900 m elevation in Wyoming and above 2,400 m in Colorado and Utah (Koehler and Brittell 1990).

In these habitats, lynx typically occur where low topographic relief creates continuous forest communities of varying stand ages. These features are most prevalent at northern latitudes but they also appear to be important components of lynx habitat in the mountains of the western United States. In both areas, such conditions are important for maintaining hare populations needed to support stable lynx populations. Habitat continuity, or the degree of habitat fragmentation, may also influence lynx population dynamics. Vast expanses of successional forests at northern latitudes support periodic population booms and crashes in numbers of hares. At southern latitudes, however, habitats are more fragmented and discontinuous resulting in lower, but more stable, hare populations (Chitty 1950; Dolbeer and Clark 1975; Koehler 1990; Sievert and Keith 1985; Windberg and Keith 1978; Wolfe et al. 1982; Wolff 1980).

Lynx habitat in the western mountains consists primarily of two structurally different forest types occurring at opposite ends of the stand age gradient. Lynx require early successional forests that contain high numbers of prey (especially snowshoe hares) for foraging and late-successional forests that contain cover for kittens (especially deadfalls) and for denning (Brittell et al. 1989, unpubl.; Koehler and Brittell 1990). Intermediate successional stages may serve as travel cover for lynx but function primarily to provide connectivity within a forest landscape. Although such habitats are not required by lynx, they "fill in the gaps" between foraging and denning habitat within a landscape mosaic of forest successional stages.

Foraging Habitat

Stand Age

Early successional forests where snowshoe hares are plentiful are the habitats that lynx favor for hunting. Such forests may result from fires (Bailey et al. 1986; Fox 1978; Keith and Surrendi 1971; Koehler 1990, 1991), timber harvesting (Conroy et al. 1979; Koehler 1990, 1991; Litvaitis et al. 1985; Monthey 1986; Parker et al. 1983; Wolfe et al. 1982), or windthrow and disease (Koehler and Brittell1990).

Based on hare pellet counts in Washington, Koehler (1990) found that hares were more abundant in younger-aged stands of lodgepole pine than in any other forest type. Hares were 4-5 times more abundant in 20-year-old lodgepole pine stands than in 43- and 80-year-old stands, and 9 times more abundant than in stands >100 years old. In Newfoundland, hares began to use cutover areas when stands reached 10 years of age, but frequency of use peaked when the stands were 22 years old (Dodds 1960). In Nova

Scotia, Parker et al. (1983) estimated hare densities at 10/ha in mid-successional habitats (16-30 years old), compared to 5.8/ha in mature conifer habitats. In Maine, hare activity was greater in 12- to 15-year-old clearcuts than in younger stages (Monthey 1986). On the Kenai National Wildlife Refuge in Alaska, hares used areas burned in 1947 more intensively than alder-dominated stands, an area burned in 1969, or mature forests, presumably because the latter habitats lacked adequate food and cover (Bailey et al. 1986).

Stand structure appears to strongly influence recolonization by hares. One year after a wildfire in Alberta, where prefire cover density was 86%, hares recolonized an intensively burned site after seedling and shrub cover approached 61% (Keith and Surrendi 1971). In this study, aspen and balsam poplar recovered quickly by sprouting. This contrasts to findings in Maine where clearcut areas initially experienced a decline in hares, and it wasn't until 6-7 years after spruce and fir became reestablished that hares recolonized the area, peaking in numbers 20-25 years later (Litvaitis et al. 1985). Litvaitis et al. (1985) found that clearcutting improved habitat quality for hares in mature forest stands where understory stem density was low.

The capacity of burned areas to support high densities of hares, and therefore lynx, undoubtedly declines over time (Fox 1978). Because succession progresses slowly at northern latitudes, older-aged (~40 years old) stands there may provide optimal conditions for hares, whereas at southern latitudes, younger-aged stands (15-30 years old) appear to provide the best habitat for hares.

Tree Species Composition

Conifer stands provide greater concealment from predators, lighter snowpacks, and warmer temperatures during winter than hardwood stands (Fuller and Heisey 1986). In Minnesota, hares used habitats with a conifer overstory and a low-growing understory, a pattern that was particularly evident during periods of hare scarcity (Fuller and Heisey 1986). Conifer cover proved to be an important habitat component for hares during a decline in Nova Scotia as well (Parker et al. 1983). In Alaska, thickets that served as refugia during periods of hare scarcity were dominated by black spruce, whereas burned areas dominated by herbaceous woody plants were occupied only during periods of hare abundance (Wolff 1980). In Maine, Monthey (1986) observed hares selecting conifer stands and Litvaitis et al. (1985) found that individual conifer stems provided about 3 times more cover than leafless hardwood stems. They also documented a strong positive correlation between the number of hares live-captured in the spring and the density of conifer stems; there was no statistical correlation with the density of hardwoods or with total stem density. Wolfe et al. (1982) concluded that dense stands of aspen in the Rocky Mountains represented marginal habitat for hares because such stands do not provide adequate cover. These studies strongly indicate that conifer cover is critical for hares during the winter.

Litvaitis et al. (1985), however, found that in coastal locations in Maine, hares preferred low-density hardwood stands where lateral foliage density was greater than in conifer stands, and that hares avoided mixed stands with an open understory. In the mountainous inland region of the state, however, hares preferred conifer stands with higher stem densities than those found in hardwood stands.

Even at southern latitudes, where hare population cycles may not occur, conifer cover is an important habitat component (Dolbeer and Clark 1975; Koehler 1990; Pietz and Tester 1983). In Colorado and Utah, dense stands of subalpine fir and Engelmann spruce and Douglas-fir were used most frequently by hares (Dolbeer and Clark 1975; Wolfe et al. 1982); in Montana, dense stands of Douglas-fir were selected (Adams 1959); and in Washington, dense stands of lodgepole pine were used most often (Koehler 1990, 1991), indicating that stem density is more important to hares than species of conifer.

Stem Density

In Washington, Koehler (1990) found a significant correlation between hare densities and stands with tree and shrub stems that were less than 2.5 cm in diameter at breast height (DBH); intensively used 20-year-old stands had 15,840 stems/ha (1.6 stems/m^2). In Alaska, Wolff (1980) found that hares preferred stands with tree and shrub densities of 22,027 stems/ha, and in Nova Scotia, hares frequented stands with stem densities of 9,000 conifers/ha (0.9/m^2) and 7,000 hardwoods/ha (0.7/m^2) (Parker et al. 1983). In Maine, hares preferred stands dominated with stems > 0.5 m tall and ≤ 7.5 cm DBH at densities > 16,000 stems/ha (1.6/m^2), with an understory visual obstruction > 60% (Litvaitis et al. 1985). Monthey (1986) also found hares to be common in densely stocked stands (stems < 8.9 cm DBH and > 0.6 m tall with 6,000-31,667 stems/ha [0.6-3.2 stems/m^2]) in Maine. In Utah, hares

seldom used stands with understories having < 40% visual obstruction during winter (Wolfe et al. 1982).

Stem Height

Because snow depths typically exceed 1 m in boreal forests, the height of stems is also an important component of winter habitat. In Minnesota, Pietz and Tester (1983) found a positive correlation between the percentage of shrub cover > 1 m tall and numbers of winter hare pellets. In Nova Scotia, habitats with stem heights between 2-3 m were important for hares, whereas mature forests with stem heights of 6-8 m and browse height < 1.0 m provided inadequate winter habitat (Parker et al. 1983). In the Rocky Mountains, where snow depths may exceed 1.5 m, Dolbeer and Clark (1975) found that sparsely stocked stands provided little food or cover, and Wolfe et al. (1982) reported that 85% of habitats used by hares had a horizontal cover density of 40% at a height of 1.0-2.5 m above the ground. In central Wisconsin, however, where snow depths may be less, Sievert and Keith (1985) concluded that stands with a dense cover of stems < 1.5-m tall provided good habitat for hares.

During snow-free periods, thermal cover is not a critical factor and alternate sources of food are available. During these times, hares will occupy habitats that are more open and where hardwoods and herbaceous vegetation are more prevalent (Dodds 1960; Litvaitis et al. 1985; Parker et al. 1983; Wolfe et al. 1982). During snow-free months, Parker et al. (1983) and Adams (1959) reported that hares avoided very dense stands where shade created by a dense canopy reduces the growth of herbaceous understory vegetation.

Denning Habitat

For denning, females select dense, mature forest habitats that contain large woody debris, such as fallen trees or upturned stumps, to provide security and thermal cover for kittens (Berrie 1973; Koehler 1990; Koehler and Brittell 1990; Kesterton 1988; Murie 1963). In north-central Washington, lynx denned in stands ≥ 200 years old with Engelmann spruce-subalpine fir-lodgepole pine overstories having N-NE aspects; these sites also had a high density (> 1/m) of downed trees supported 0.3-1.2 m above the ground, which provided both vertical and horizontal structural diversity (Brittell et al. 1989, unpubl.; Koehler 1990). Other important features of denning sites are minimal human disturbance, proximity to foraging habitat (early successional forests), and stands that are at least 1 ha in size (Koehler and Brittell 1990). Travel corridors between den sites are important to permit females to move kittens to areas where prey are more abundant or to avoid disturbance (Koehler and Brittell 1990).

In areas where denning habitat is abundant, female lynx often change denning sites during and between seasons (Washington Dept. of Wildlife 1993, unpubl.). Where high-quality denning habitat is scarce, however, lynx may re-use the same denning site (pers. Comms. By Brittell and Slough cited in Washington Dept. of Wildlife 1993, unpubl.). The availability of alternate den sites may be an important determinant of habitat quality. In low-quality habitat, the inability of females to move kittens to alternate dens when danger threatens may increase mortality rates for kittens. According to Brittell et al. (1989, unpubl.), den sites consisting of mature forest habitat are also important for lynx as refugia from inclement winter weather or drought.

Travel Cover

Like most wild felids, lynx require cover for security and for stalking prey; they avoid large, open areas. Although lynx will cross openings ≤ 100 m in width, they do not hunt in these areas (Koehler 1990; Koehler and Brittell 1990). Travel cover allows for movement of lynx within their home ranges and provides access to denning sites and foraging habitats (Brittell et al. 1989, unpubl.). In general, suitable travel cover consists of coniferous or deciduous vegetation > 2 m in height with a closed canopy that is adjacent to foraging habitats (Brittell et al. 1989, unpubl.). Lynx are known to move long distances but open areas, whether human-made or natural, will discourage use by lynx and disrupt their movements. Thus, maintaining travel corridors between populations may be important to ensure the long-term viability of peripheral or isolated populations in the western mountains (Koehler 1990; Koehler and Brittell 1990).

Roads constructed for forest management, mining, or recreational purposes may increase the vulnerability of lynx to hunters and trappers (Bailey et al. 1986; Todd 1985) and increase opportunities for accidental road deaths (Brocke et al. 1992). During winter and summer, lynx frequently travel along roadways with < 15 m right-of-ways, where adequate cover is present on both sides of the road (Koehler and Brittell 1990). Although forbs, grasses, and shrubs that grow along edges of roads can benefit hares and attract

lynx, increased access and use of roadways by people may pose a threat to lynx populations, particularly during times of high pelt prices and low recruitment (Bailey et al. 1986).

Although sparsely stocked stands are poor habitat for hares, they may benefit lynx by serving as dispersal sinks in which juvenile hares are more vulnerable to predation (Dolbeer and Clark 1975; Sievert and Keith 1985; Windberg and Keith 1978). For these reasons, an interspersion of dense stands that provide refugia for hares, and sparsely stocked stands where hares are more vulnerable, may be more beneficial to lynx than a continuous distribution of optimal hare habitat.

Because plant succession progresses more rapidly at southern latitudes, small-scale disturbances at frequent intervals may be necessary to provide for a temporal continuum of stand ages. Fires, epidemics of forest disease, and logging may have negative short-term effects by eliminating cover for snowshoe hares and lynx, but will have long-term benefits as succession progresses, cover is restored, and snowshoe hares become abundant (Koehler and Brittell 1990; Parker et al. 1983).

Management Considerations

1. High-quality lynx habitat in the western mountains consists of a mosaic of early successional habitats with high hare densities, and late-successional stands with downed woody debris for thermal and security cover and for denning.

2. Clearcuts >100 m wide may create barriers to lynx movements.

3. Hares may not begin to recolonize Clearcuts until 6-7 years after cutting, thus it may take 20-25 years at southern latitudes for snowshoe hare densities to reach highest levels.

4. Thinning stands early to maximize tree-growth potential can be compatible with snowshoe hare and lynx habitat needs provided that stands are thinned before snowshoe hares recolonize the area. Otherwise, thinning may be most effective when stands are older than 30-40 years and are used little by hares. Both early and late thinning strategies may be required when integrating timber management objectives with lynx habitat needs.

5. Small-sized parcels (1-2 ha) of late-successional forest appear to be adequate for den sites, but these parcels must be connected by corridors of cover to permit females to move kittens to alternate den sites providing suitable access to prey.

6. Approximating the natural disturbance frequency and spatial patterns present on the landscape is expected to provide the best habitat for lynx. Frequent, small-scale disturbances is expected to provide the best lynx habitat at southern latitudes.

7. Although disease and insect attacks may increase fuel loads and the risk of large, high-intensity fires, they also provide dead and downed trees used for denning cover. Thus, the role that disease and insects play in the dynamics of forests being manipulated must be carefully considered when managing stands for timber and lynx.

8. Road management is an important component of lynx habitat management. Although construction and maintenance of roads both destroys and creates habitat for prey, lynx use roads for hunting and travel which may make them more vulnerable to human-caused mortality.

Research Needs

1. Studies of lynx distribution and habitat use in the western mountains are urgently needed. Gathering this information will require winter surveying of remote areas in winter where lynx are believed to occur and evaluating patterns of occurrence with geographic information systems (GIS). GIS can then be used to inventory available habitats on a regional scale. Once this is achieved, more intensive field investigations of habitat use, spatial patterns, and reproductive ecology using radiotelemetry will be appropriate.

2. Forest management activities, timber harvesting, and prescribed and wild fires can be either detrimental or beneficial to lynx, depending upon their scale and dispersion on the landscape. Although guidelines exist, it will require some experimentation to determine prescriptions that provide an optimal range and pattern of habitat patchiness to benefit both hares and lynx. Such experimentation will require long-term research and monitoring of both lynx and snowshoe hare populations.

HOME RANGE AND MOVEMENTS

Home Range

Lynx partition resources both spatially and temporally, but determining the social and spatial organization of solitary felids is difficult. Most studies do not encompass a long enough time period nor do they include an adequate sample of individuals. These

limitations result from the difficulties involved in (1) capturing and marking individuals occupying adjacent home ranges, and (2) obtaining representative samples of sex and age classes. However, certain patterns can be detected from the studies that have been. conducted. Although lynx are considered to be solitary, they frequently travel in groups, such as females with kittens, two adult females with their litters, or females traveling with males during the breeding season (Carbyn and Patriquin 1983; Parker et al. 1983; Saunders 1963b).

Snow-tracking and radiotelemetry studies have been used to delineate spatial requirements of lynx and to assess spatial partitioning between and within sexes. Nellis et al. (1972) identified areas used by lynx as activity centers that were separated in time and space. Radiotracking studies by Parker et al. (1983) support the concept of lynx using activity centers during winter. They documented both males and females concentrating 75% of their activity in core areas, which ranged from 35-63% of winter home ranges. Although in Alaska, Kesterson (1988) found that lynx in Alaska occupied intrasexually exclusive areas, spatial overlap among individuals is common (Bergerud 1971; Brand and Keith 1979; Koehler 1990; Saunders 1963b; Ward and Krebs 1985), and it is generally believed that lynx occupy home range areas rather than exclusive territories.

Factors that influence the size and shape of home ranges are not fully understood, but it is generally believed to be related to the availability of prey and the density of lynx. Other factors that may contrib.-ute to the size and configuration of home range areas include geographic and physiographic features. Saunders (1963b) found that home range boundaries coincided with habitat features, and Koehler (unpubl. data) observed home range areas in a mountainous region of Washington to correspond to drainage patterns, with home range boundaries generally occurring along ridges and major streams. Therefore, physiographic features and variation in the distribution of habitats may partially account for differences in home range sizes between geographic areas.

Ward and Krebs (1985) demonstrated a correlation between prey density and lynx home range sizes in the Yukon by using radiotelemetry. As numbers of hares decreased from 14.7 to < 1 /ha, the mean home range size for lynx increased from 13.2 to 39.2 km^2, a 3-fold increase in home range size in response to a 14-fold decrease in hare abundance. Similarly, Poole (1993, unpubl.) found lynx home ranges increased from 17 km^2 to 25-84 km^2 as hare numbers dropped, with the majority of lynx becoming nomadic or emigrating at that time. Such observations of lynx changing their use of space in response to declining numbers of hares is in contrast to findings by Breitenmoser et al. (1993), however, which showed no change in the size of home ranges between periods of high and low hare numbers. In addition, snow-tracking studies by Brand et al. (1976) indicated that lynx did not modify their home range sizes in response to changing numbers of hares. However, during a period of low hare densities in interior Alaska, Perham et al. (1993, unpubl.) observed some lynx hunting in isolated pockets of hare activity and occupying small home ranges, whereas others became nomadic or emigrated. Slough and Mowat (1993, unpubl.) found that mean annual home range sizes varied from 8.3 to 18.2 km^2 for females and from 17.3 to 51.0 km^2 for males as hare numbers increased from 1982 to 1992. They hypothesized that lynx maintained intrasexual territories during hare lows, but that this intolerance broke down as hare numbers increased.

A variety of techniques has been used to calculate the size of home range areas, and each technique can result in different estimates. For example, snow-tracking generally results in smaller home ranges from those calculated from radiotelemetry studies. Furthermore, the number of locations used generally differs between studies and can affect area determination (Mech 1980; White and Garrott 1990). For these reasons, caution must be applied when comparing home range sizes between different studies.

Studies using radiotelemetry have estimated home ranges for lynx varying in size from 8 to 783 km^2 (Berrie 1973; Bailey et al. 1986; Brainerd 1985; Brittell et al. 1989, unpubl.; Carbyn and Patriquin 1983; Kesterson 1988; Koehler 1990; Koehler et al. 1979; Parker et al. 1983; Perham et al. 1993, unpubl.; Poole 1993, unpubl.; Slough and Mowat 1993, unpubl.; Smith 1984; Ward and Krebs 1985). Based on snow-tracking, lynx occupy areas from 15.4 to 20.5 km^2 in Newfoundland (Saunders 1963b), and 18 to 49 (average 38.4) km^2 in Alberta (Nellis et al. 1972). On the same study area in Alberta, Brand et al. (1976) estimated that home range size varied from 11.1 to 49.5 kmz (average 28.0 km^2).

Although large home ranges are generally associated with low numbers of prey, they may also occur in areas into which lynx have recently immigrated (Mech 1980) or that are heavily trapped (Bailey et al. 1986; Carbyn and Patriquin 1983). In Manitoba, home

ranges used by two females during winter averaged 156 km^2 while that for a male was 221 km^2 in an area that was intensively trapped (Carbyn and Patriquin 1983). Their study area of 2,144 km^2 was an isolated refuge surrounded by agricultural land that was only occasionally colonized by immigrating lynx. On the Kenai Peninsula in Alaska, where lynx were heavily exploited, Bailey et al. (1986) found home ranges for two females to be 51 and 89 km^2 and that for one male to be 783 km^2. As lynx densities increased after the trapping season was closed, sizes of lynx seasonal home ranges decreased 54.7% for resident males and 36.9% for nondenning, resident females (Kesterson 1988). During a period of increasing hare numbers in Nova Scotia, an adult female used an area of 32.3 km^2 and an adult male, 25.6 km^2 (Parker et al. (1983).

Lynx that had immigrated into Minnesota where hares were scarce occupied areas of 51-122 km^2 for females and 145-243 km^2 for males (Mech 1980). Lynx translocated to an area of low hare density (mean of 0.5 hares/ha) in New York also had large home ranges, with harmonic mean estimates of 1,760 km^2 for 21 males and 421 km^2 for 29 females (Brocke et al. 1992). In this area, 73% of known mortalities were human-caused. This high level of mortality was believed to have resulted from fragmented property ownership and many access roads. In Washington, where hares were relatively scarce and suitable habitats scattered, home range sizes averaged 39 km^2 for 2 females and 69 km^2 for 5 males (Koehler 1990). In western Montana, the mean home range size for 4 lynx (2 males and 2 females) was 133 km^2 (Smith 1984). In a subsequent study in the same area, Brainerd (1985) radio-collared 7 lynx and measured mean annual home ranges of 122 km^2 for males and 43.1 km^2 for females.

Lynx will maintain home ranges for several years. In Washington, site fidelity was observed for more than 2 years (Koehler 1990) and in the Yukon, a male was observed using the same area for at least 10 years (Breitenmoser et al. 1993). Radiotelemetry studies show that home range sizes vary by season. In Alaska, females occupied smaller areas in summer (25 km^2) than in winter (49 km^2) (Bailey et al. 1986). The opposite relationship was documented in Nova Scotia, however, where an adult female expanded her home range from 18.6 km^2 in winter to 32.3 km^2 in summer, and an adult male from 12.3 km^2 in winter to 25.6 km^2 in summer; there was little seasonal change for a juvenile (10.1 km^2 in winter and 7.9 km^2 in summer) (Parker et al. 1983). Prior to dispersing, a juvenile male occupied a home range in Alaska of 8.3 km^2 in an area providing high-quality hare habitat (Bailey et al. 1986). In one of the few studies conducted in mountainous terrain, Koehler (1990) found that lynx in north-central Washington used significantly higher elevations during summer (range 1,463-2,133 m) than in winter (range 1,556-2,024 m). The extent of home range overlap for lynx is variable. Ward and Krebs (1985) found male home ranges to overlap those of other males by 10.5%, among females by 24.5%, and between males and females by 22.0%. However, in Washington, Koehler (1990) found home ranges of males and females to overlap completely, particularly during March and April when breeding occurred (Koehler, unpubl. data). Parker et al. (1983) also documented complete overlap in home ranges of radio-collared males and females, and Mech (1980) found complete overlap among radio-collared females but not among males, although there may have been overlap with uncollared males. Kesterson (1988), however, observed little overlap in home range use among females (mean overlap, 5.0%) or among males (3.8%); however, male ranges overlapped those of 1-3 females.

Movements and Dispersal

When hares are scarce, several lynx may congregate around pockets of dense vegetation or on caribou calving grounds where prey resources are more plentiful (Bergerud 1971; Ward and Krebs 1985). During such times, the spatial and temporal segregation of lynx may cease to exist, and some lynx may abandon their home range areas and become nomadic or emigrate in search of prey (Poole 1993, unpubl.; Ward and Krebs 1985). Records indicate long-distance movements by lynx of 1,100 km (Slough and Mowat 1993, unpubl.) and 700 km (Ward and Krebs 1985) in the Yukon, 930 km in the Northwest Territories (Poole 1993, unpubl.), 616 km in Washington (Brittell et al. 1989, unpubl.), 325 km in western Montana (Brainerd 1985), 483 km in Minnesota (Mech 1977), 164 km in Alberta (Nellis et al. 1972), and 103 km in Newfoundland (Saunders 1963b). Translocated lynx in New York used areas exceeding 1,000 km^2 (Brocke et al. 1992).

Ward and Krebs (1985) considered the abandonment of home range areas and nomadic behavior to be related to decreased hare densities, especially when hare densities dropped below 0.5/ha. In the Yukon, Slough and Mowat (1993, unpubl.) found

annual immigration and emigration rates to be relatively constant at 10-15%, with most juvenile males dispersing and juvenile females tending to remain on their natal ranges, although emigration increased to 65% with no apparent immigration as hare numbers crashed. In the Northwest Territories, kittens and yearlings began dispersing during the peak in hare numbers, while emigration of adults didn't occur until after the crash in hare numbers (Poole 1993, unpubl.).

These long-range movements may serve to repopulate vacated areas or to augment depauperate populations along the southern edge of the lynx's range. After a long period of heavy trapping pressure, lynx populations increased during the 1960's in Alberta (Todd 1985) and in eastern Montana (Hoffmann et al. 1969). As is indicated by the failure of lynx to establish themselves in Minnesota after immigrating- there in large numbers in the early 1970's (Mech 1980), however, such movements are unlikely to result in stable lynx populations unless available habitats are capable of supporting both snowshoe hares and lynx in sufficient numbers for population persistence.

During the 1970's, heavy trapping pressure probably resulted in overexploitation of lynx populations in Ferry County, Washington, yet only recently does it appear that lynx have recolonized that area (Washington Dept. of Wildlife 1993, unpubl.; Koehler, pers. obs.). Lynx habitat in Ferry County is separated from suitable habitat in British Columbia by the Kettle River drainage and xeric non-lynx habitats that may act as barriers to lynx dispersal and recolonization. Extensive fires, logged areas, and forest disease control programs may also act to inhibit immigration of lynx into suitable habitat (Koehler 1990; Koehler and Brittell 1990).

Translocation may be a viable alternative for reestablishing lynx populations into areas where they occurred historically, but reintroductions are problematic. Of 50 lynx translocated from Yukon Territory to the Adirondack Mountains of New York, 6 animals were killed on roads, 2 were shot, and 3 young lynx died from natural causes (Brocke et al. 1992). The home range sizes of translocated animals were very large, averaging 1,760 km^2 for males and 421 km^2 for females, suggesting that they exhibited the unsettled behavior of recently translocated animals, which may make them more vulnerable to both human-related and natural mortality (Brocke et al. 1992). The authors suggest that large, continuous blocks of public land, with minimal development or roads providing vehicular access, will be critical for the survival of reintroduced lynx.

Management Considerations

1. Differences in the home range requirements and social organization of lynx in different areas indicate that management is best considered at regional levels, rather than provincial or state levels. Considering the role that emigration may play in population dynamics at a regional scale, it is also important to recognize that management activities in one area may affect populations in neighboring and outlying regions.

2. Habitat management for lynx would benefit from a consideration of local home range sizes and distributions, and vegetative and physiographic features which may serve as home range boundaries.

Research Needs

1. Many authors have suggested that periodic irruptions of lynx in Canada, resulting in the emigration of lynx to peripheral areas outside of their core range, are an essential factor in the maintenance of marginal populations. Although they will be extremely difficult to conduct, studies are needed to assess the importance of immigration on the demographics and persistence of peripheral populations.

COMMUNITY INTERACTIONS

The lynx is a specialized predator of snowshoe hares; its geographic distribution, the habitats it selects, its foraging behavior, reproductive capacity, and population density are all affected by the distribution and abundance of the snowshoe hare. The snowshoe hare is also an important part of the diet of several other predators in boreal forests of North America. In central Canada, hares may comprise 20.4-51.8% of the winter diet of marten (*Martes americana*) (Bateman 1986; Thompson and Colgan 1987) and hares are also potentially important in the diets of fishers (*Martes pennanti*) and, to a lesser extent, wolverines (*Gulo gulo*). Their different foraging strategies and use of habitats, however, may minimize opportunities for competition for prey between these species and lynx (see chapters on marten, fisher, and wolverine). At northern latitudes, coyotes, red foxes, and several species of raptors also prey on

hares, and at southern latitudes, bobcats may also be significant competitors.

Other mammalian predators and raptors that prey on hares may contribute to increased mortality and depressed populations of hares, which could affect the availability of prey for lynx (Boutin et al. 1986; Dolbeer and Clark 1975; Keith et al. 1984; Sievert and Keith 1985; Trostel et al. 1987; Wolff 1980). In southwest Yukon, hares comprised 86.2 and 77.0% of coyote and red fox diets, respectively (Theberge and Wedeles 1989). Coyotes also preyed on hares in Alaska during winter, where hares occurred in 16% of coyote scats and 64% of lynx scats examined (Staples and Bailey 1993, unpubl.). Keith et al. (1984) found lynx to kill 0.8 hares/day, coyotes 0.6/day, and great horned owls 0.35/day; half of the mortality of radio-collared hares was attributed to coyote kills. At southern latitudes, Litvaitis and Harrison (1989) found snowshoe hare remains in 64.7-84.0% of bobcat diets and 29.3-66.7% of coyote diets.

Although their diets may overlap, differences in habitat selection may minimize competition for prey resources by lynx and other predators, especially during winter. Measurements show the relative support capacity of lynx paws to be twice that for bobcat paws (Parker et al. 1983) and 4.1-8.8 times that of coyote paws (Murray and Boutin 1991), enabling lynx to exploit high-elevation areas where deep snow would exclude coyotes and bobcats (Brocke et al. 1992; Koehler and Hornocker 1991; Murray and Boutin 1991; Parker et al. 1983). However, opportunities for resource overlap among these species may increase during winter due to increased access to high-elevation habitats via snowmobile trails and roads maintained for winter recreation or forest management activities. Increased competition from other predators may be particularly detrimental to lynx during late winter when hare numbers are lowest and lynx are nutritionally stressed.

Management Considerations

1. Because the ranges of lynx, bobcats, and coyotes overlap in the western mountains, competition for snowshoe hares and other prey species may be of significant management concern.

Research Needs

1. Determine the extent to which lynx compete with other predators for prey, and under what conditions competition may adversely affect lynx populations.

CONSERVATION STATUS IN THE WESTERN MOUNTAINS

Lynx populations in the western mountains of the United States occur at the periphery of the species' range in North America. At high elevations, climatic conditions similar to those occurring at higher latitudes support boreal forests, snowshoe hares, and lynx. Populations in this region, particularly those found in Wyoming, Utah, and Colorado, exist at low densities in fragmented and disjunct distributions. Although habitats at high elevations in the western mountains are sufficient to support this boreal community, ecological conditions there vary in significant ways from those in boreal regions of Canada and Alaska. Because of the fragmented nature of habitat and the presence of facultative predators and potential competitors in the western mountains, snowshoe hare populations and, consequently, lynx populations do not exhibit dramatic population cycles (Koehler 1990). In the western mountains, populations of both species occur at densities comparable to those found during hare population lows in Canada and Alaska. Additionally, available evidence indicates that lynx food habits, natality and mortality rates, habitat use, and spatial patterns in the western mountains are comparable to those occurring in the north when hare populations are at low densities.

Lynx are vulnerable to trapping, and the effect of trapping mortality on population numbers appears to be largely additive, not compensatory. Brand and Keith (1979) speculated that during hare population lows when recruitment in lynx populations is low, intensive trapping of lynx could result in local extinctions. These authors recommended that trapping of lynx in northern boreal forests should cease during the 3-4 years when hare populations are at their lowest levels. Because hare populations are always at generally low levels in the western mountains, this line of reasoning suggests that complete protection of lynx populations in the western states may be appropriate to ensure their population persistence.

Lynx are protected in Wyoming, Utah, and Colorado, and Washington closed the lynx harvest in 1991 when the north Cascades lynx population was petitioned for federal listing as endangered. The petition was denied (Federal Register 1992, 1993), but Washington State classified the lynx as threatened in October 1993 (Washington Dept. of Wildlife 1993, unpubl.).Lynx are still classified as furbearers in Idaho and Montana, although strict harvest quotas are imposed (table 2).

The range of lynx in the western mountains has diminished over the last century, suggesting that lynx may be negatively impacted by development. Because suitable habitats are more fragmented and restricted in extent in the western mountains, lynx may be less tolerant of human activities there than in Canada and Alaska, where refuge habitats are more prevalent. Thus, providing protected areas within optimal lynx habitat in the western mountains may be important for the persistence of lynx populations. Landscape-level research using radio-telemetry and GIS analyses are needed to study the effects of human activity on lynx populations.

It is of critical importance to the conservation of lynx in the western mountains to evaluate the extent to which these populations are tied to source populations in Canada. Emigrating lynx appear to have very low survival rates. Are southern populations augmented periodically by lynx moving in from the north, or are they simply maintained at low levels by habitat limitations and unaffected by such immigration? Will international cooperation involving lynx population management be required, or should efforts be directed at habitat management at the local or regional level? Answers to these questions will be essential to the design of management strategies for lynx, especially in Washington, Idaho, and Montana.

Only five lynx studies have ever been conducted in the western mountains of the United States, including two in Washington and three in Montana (table 3). These studies have been concerned mainly with home range characteristics and habitat use; information on demography, food habits, dispersal, and denning sites is almost totally lacking. Additional research on lynx in the western mountains, especially studies of their foraging ecology, den site characteristics, and habitat relationships at the landscape scale, are urgently needed. The conservation of such a wide-ranging and specialized predator will require a significant commitment of resources to obtain the information needed to maintain viable populations in the western United States.

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Table 3.--Studies of lynx in the western mountains of the United States, excluding Alaska, by subject. Only studies for which the subject was an objective of the study are listed; incidental observations are not included. Sample size is number of animals or carcasses studied or, for food habits, number of scats or gastrointestinal tract contents examined. Dispersal refers only to movements away from the mother's home range by juveniles; data on emigration by adults are not included. Separate studies are indicated with an asterisk (*).

Topic, author	Location	Method	Duration	Sample size
Home range and habitat use				
*Brittell et al. 1989, unpubl.	NE Washington	Telemetry (hr)[1]	34 months	15
*Koehler 1990	NE Washington	Telemetry (hr)	25 months	7
*Koehler et al. 1979	NW Montana	Telemetry (hr)	8 months	2
*Smith 1984	W Montana	Telemetry (hr)	23 months	4
*Brainerd 1985	W Montana	Telemetry (hr)	25 months	7
Demography				
Brainerd 1985	W Montana	Carcasses	4 trapping seasons	20
Food habits				
Koehler 1990	NE Washington	Scats	25 months	29
Dispersal				
None				
Natal dens				
Koehler 1990	NE Washington	Telemetry	25 months	4 dens; 2 females

[1] *(hr) = home range size reported.*

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Chapter 5

Wolverine

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INTRODUCTION

The wolverine (*Gulo gulo*) is the largest-bodied terrestrial mustelid. Its distribution is circumpolar; it occupies the tundra, taiga, and forest zones of North America and Eurasia (Wilson 1982). North American wolverines are considered the same species as those in Eurasia. They are usually thought of as creatures of northern wilderness and remote mountain ranges. In fact, wolverines extend as far south as California and Colorado and as far east as the coast of Labrador, although low densities are characteristic of the species.

Relative to smaller mustelids, the wolverine has a robust appearance, rather like a small bear. Its head is broad and rounded, with small eyes and short, rounded ears. The legs are short, with five toes on each foot. The claws are curved and semi-retractile and are used for climbing and digging. The skull and teeth are robust and the musculature, especially of the head, neck and shoulders, is well developed. These adaptations allow the wolverine to feed on frozen flesh and bone (Haglund 1966). Typical weights for adult males are 12-18 kg and for adult females, 8-12 kg. Adult males are 8-10% larger in measurements and 30-40% larger in weight than females.

The coat is typically a rich, glossy, dark brown. Two pale buff stripes sweep from the nape of the neck along the flanks to the base of the long, bushy tail. The fur on the abdomen is dark brown. White or orange patches are common on the chest or throat. Occasionally the toes, forepaws or legs are marked with white. Color can vary strikingly, even within the same geographical area, from a pale brown or buff with well defined lateral stripes to a dark brown or black with faint or no lateral stripes. Very blond or "white" wolverine are rare. Because of the extensive within-site color variation, geographical differences in color do not seem to be apparent, except for possibly greater incidence of white markings in some areas. Color does not vary markedly with season. A single visible moult extends from spring or early summer to autumn (Obbard 1987). Age and sex differences are seldom described, but Holbrow (1976) suggested that younger animals may be darker.

The wolverine has been characterized as one of North America's rarest mammals and least known large carnivores (table 1). Only four North American field studies have been completed: two in Alaska (Gardner 1985; Magoun 1985) and one each in the Yukon (Banci 1987) and Montana (Hornocker and Hash 1981). Additional studies, including one in Idaho, Alaska, and the Yukon are in progress (table 1). Reproduction and food habits of northern wolverine have been described from analyses of carcasses (table 1). Information on the habitat and population ecology of wolverines in the forests of western North America is mainly anecdotal or not available. Because of reductions in numbers and in distributions, increasing emphasis is being given in some western North American areas such as California, Colorado, and Vancouver Island, British Columbia, as to whether wolverine still occur. The paucity of information is largely due to the difficulty and expense of studying a solitary, secretive animal that is rare compared to other carnivores, and is usually found in remote places.

The wolverine's importance to humans began with the fur trade. Wolverine fur is renowned for its frost-resistant qualities (Quick 1952) and is sought for use as trim on parkas, especially by the Inuit of Canada and Alaska. Although wolverine fur typically is not used for making coats, it is commonly used in rugs and taxidermic mounts. The names by which wolverine are known are colorful and descriptive. The Cree names *ommeethatsees*, "one who likes to steal" and *ogaymotatowagu*, "one who steals fur" (Holbrow 1976), refer to wolverine raiding traplines, cabins and caches, and removing animals from traps. They are called "skunk-bears" because they mark the food they kill or claim, including the contents of cabins, with musk and urine. "Glutton" refers to its mytho-

Table 1.--The knowledge base for the wolverine in North America 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. Individual studies are represented by (*) discounting redundancies.

Topic, author	Location	Method	Duration (years)	Sample size	Note
Home range & habitat use					
*Hornocker and Hash 1981	NW Montana	Telemetry	7	24	
*Gardner 1985	SC Alaska[1]	Telemetry	4	12	
*Magoun 1985	NW Alaska	Telemetry	4	19	
*Banci 1987	SW Yukon	Telemetry	4	10	
Demography					
*Wright & Rausch 1955	Alaska	Carcasses	4	33	
*Bausch & Pearson 1972	Alaska & Yukon	Carcasses	5	697	
*Llskop et al. 1981	N British Columbia	Carcasses	2	90	
Gardner 1985	SC Alaska[1]	Carcasses	3	71	
Magoun 1985	NW Alaska	Carcasses	4	67	
Band & Harestad 1988	Yukon	Carcasses	3	413	
Food Habits					
Rausch 1959	Alaska	Gut analysis	4 (winter)	20	Stomachs
Rausch & Pearson 1972	Alaska	Carcasses	5 (winter)	192	G.I. tracts
Hornocker & Hash 1981	NW Montana	Scats	6 (Dec-Apr)	56	# individuals unknown
Gardner 1985	SC Alaska[1]	Carcasses	4 (Dec-Mar)	35	Colons
Gardner 1985	SC Alaska[1]	Observations	3 (Apr-Oct)	9	Of 70 telemetry flights
Magoun 1985	NW Alaska	Scats	2 (Nov, Feb, Mar)	82	# individuals unknown
Magoun 1985	NW Alaska	Observations	4 (May-Aug)	48	Of 362 5-min. periods
Banci 1987	Yukon	Gut analysis	4 (Nov-Mar)	411	G. I. tracts
Dispersal					
Gardner 1985	SC Alaska[1]	Telemetry	4	2	2 males
Magoun 1985	NW Alaska	Telemetry	4	7	4 males
Banci 1987	SW Yukon	Telemetry	4	3	1 male
Natal Dens					
Magoun 1985	NW Alaska	Observations	4	4	3 females

[1] *Three field studies are currently In progress; Golden et al. 1993, south-central Alaska; Cooley, pers. comm., northern Yukon; Copeland 1993, north-central Idaho.*

logical voracious appetite and "Indian devil" to its importance in the legends of native cultures. The wolverine has been described as "the fiercest creature on earth" (Ferguson 1969), "vicious," a "dangerous killer," and "a fearless aggressive fighter" who "will drive bears away from their kills" (Winkley and Fallon 1974). This reputation as vicious and conflicts with trappers resulted in wolverine being considered as vermin by European-North Americans, an attitude that persisted into the 1960's.

The strength of the wolverine is legendary. Reports have it carrying away moose (*Alces alces*) carcasses and caribou (*Rangifer tarandus*) heads, destroying steel traps, and eating through wood walls and roofs. As a scavenger largely dependent on large mammal carrion, the wolverine needs the tenacity to survive long periods without food and the strength to use available food. Not a hunter, it depends on wolves and other predators to provide carrion, and contrary to legend, is at times killed by these carnivores.

Within its geographic range, the wolverine occupies a variety of habitats. However, a general trait of areas occupied by wolverines is their remoteness from humans and human developments. The wolverine is a management and conservation enigma because the attributes of wilderness upon which it depends are not known. Is food, denning habitat, solitude, or some other factor all-important? Some disturbed habitats have abundant food in the form of large mammal carrion but do not support wolverines. Wolverines can move long distances but have not recolonized Labrador and Quebec despite the abundance of caribou and undisturbed habitat. By contrast, wolverines in arctic Alaska can survive

some winters with their only food the remnants of old caribou kills, long after the caribou have migrated elsewhere.

Human presence alone is not a deterrent to the presence of wolverines, as evidenced by their feeding in garbage dumps in northern Canadian communities. If large tracts of undeveloped and unroaded habitat are essential, why do wolverine occur in the logged forests of the Sub-Boreal Interior of British Columbia and in the habitats criss-crossed with seismic lines on the Boreal Plains? (See map in Appendix A.) A combination of factors likely underlie the presence or absence of self-sustaining wolverine populations. A pressing conservation issue is that we lack knowledge of what factors allow wolverines to persist at intermediate densities in western Canadian forests, while resource managers are being asked to provide for the needs of wolverines in the western conterminous United States, where population and habitat conditions are poorly known and likely more tenuous.

CURRENT MANAGEMENT STATUS

In the United States, wolverines may be trapped for fur only in Alaska and in Montana, but in Canada, they are important furbearers in all western provinces and territories and in Ontario. Trapping seasons generally extend from October-November to February-April; seasons are longest in the North. The wolverine population east of Hudson Bay has been classified as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 1993). Harvests in Ontario are minimal and mostly incidental, in traps set for other species.

In most jurisdictions where they are trapped, wolverines have dual status as a furbearer and as big game, but hunting is an important source of mortality only in the northern Yukon, the Northwest Territories, and Alaska. Reported harvests from Alaska and the Canadian territories likely account for only one-fifth to one-third of the total harvest because of heavy unreported harvest and use by local communities (Melchoir et al. 1987). The requirement to submit pelts for sealing in the Yukon is recent and its effectiveness is unknown. Declining wolverine harvest trends throughout southcentral Alaska during the 1980's prompted managers to reduce season lengths and bag limits and to restrict harvest methods (unpublished data in Gardner et al. 1993; Becker and Gardner 1992). Concerns about overharvests have also been expressed in other areas of Alaska (unpublished data in Bangs and Bailey 1987).

Management of furbearers in British Columbia, the Yukon, and the northern parts of the prairie provinces is based on a system of registered traplines, on which individual trappers or bands are given the exclusive right to trap. This system reduces trapper effort, avoids localized over-harvests, and provides trappers with an incentive to harvest sustainably. Trapping is not permitted in national, provincial, or territorial parks. Harvests in British Columbia are monitored by mandatory reporting of furs sold by trapline. Harvesting of wolverine on Vancouver Island is prohibited. Beginning in 1993-94, seasons in southwestern British Columbia were closed, consistent with the view that furbearer populations at low densities in marginal habitats should not be trapped.

In Alberta, the southern and agricultural parts of the province are closed to wolverine trapping. Most (80-90%) of the yearly harvest in Alberta and Saskatchewan is incidental to harvests of other species, or wolverine are taken opportunistically by big game hunters (F. Neumann, W. Runge, pers. comm.). Similarly in Manitoba, 35-44% of the harvest is incidental (I. McKay, pers. comm.). In the Northwest Territories, voluntary carcass submission is used to monitor the age-sex composition of the harvest (unpublished data in Poole 1991-1992). In the Yukon (B. Slough, pers. comm.), Alberta (unpublished data in McFetridge 1991-1993), and British Columbia (unpublished data in Rollins 1993), annual trapper questionnaires are used to monitor trends in furbearer and prey abundance.

Conterminous United States

The wolverine is designated as threatened in California, endangered in Colorado, and protected in four states (Appendix C, table 4d). Petitions have been filed for listing under the U.S. Endangered Species Act for California and Idaho. It is listed by the USDA Forest Service, Regions 1, 2 ,4, and 6 as a sensitive species (Appendix C).

Other than Alaska, Montana is the only state that allows trapping of wolverines. Before 1975, the wolverine in Montana was classified as a predator and unprotected (Hornocker and Hash 1981). Since then, trapping has been limited by seasons, licensing, and a seasonal limit of one wolverine per trapper. These regulations decreased the annual harvest "markedly" (Hornocker and Hash 1981). Most of the current trap-

per harvest in Montana is believed to be incidental, in sets for other furbearers (B. Giddings, pers. comm.).

DISTRIBUTION AND TAXONOMY

Wolverines in North America are more or less a continuous breeding group from the 38th parallel northward. Because of the wolverine's extensive movements, I have used ecoprovinces (Appendix A) for examining biological variation among wolverine populations. This convention is a convenience for delineating populations on an ecological basis. It is not known whether genetic differences occur among such populations or whether they can be considered ecotypes.

Distribution

Wolverines occur across the boreal and tundra zones of Eurasia. Populations in Scandinavia have recovered from near extinction in the last two decades (Bevanger 1992; Kvam et al. 1984). However, their future is uncertain because of increasing conflicts with sheep ranchers (Bevanger 1992). Ognev (1935) believed that the distribution of wolverines in Soviet states had decreased since the 1800's, but we know little about their current status there and in other Asian countries.

In the western conterminous United States, wolverines occur in peninsular extensions of the more extensive Canadian habitat, found mostly in the Humid Continental Highlands, Semi-Arid Steppe Highlands, Temperate Semi-Desert Highlands, and Mediterranean Highlands ecodivisions (Appendix A). They appear to have been rare or absent from the Columbia Plateau, Great Basin, Wyoming Basins, and Northern Great Plains ecoprovinces, and rare within the Canadian Prairie ecoprovince in historical times (Scotter 1964).

Seton (1929) concluded that the wolverine never occurred in Nova Scotia or on Prince Edward Island and that it disappeared from New Brunswick in the second half of the 19th century. Historically, wolverines occupied Labrador and Quebec (Kelsall 1981) but not Newfoundland Island (Anderson 1946). Wolverines are thought to have had a wide presettlement distribution in the Great Lakes region, although only in small numbers (deVos 1964). They have been absent from this region since the early 1900's (deVos 1964) and are extirpated from North Dakota, Minnesota, Wisconsin, Michigan, and Iowa (Hamilton and Fox 1987). Considering the extensive movements of wolverines, it is likely that individuals have been observed in areas that could not support home ranges or reproduction.

Wolverines in the Manitoba part of the Aspen Parkland ecoprovince (Appendix A) were rare (van Zyll de Jong 1975), and those in the Alberta part had disappeared by the early 1930's (Soper 1964). The wolverine's current range in Manitoba, generally north of 54°, includes much of the estimated range in 1909 (Seton 1909) but excludes areas that have been farmed or cleared. The distribution in northern Saskatchewan coincides with that of barren-ground caribou-the southern Taiga Shield ecoprovince and the forests of the Boreal Plains (W. Runge, pers. comm.). Wolverines in Alberta have been extirpated from the extensively modified Boreal Plains and currently only occur in the Taiga Plains and Shining Mountains ecoprovinces. In the latter, populations coincide with and may have been maintained by the extensive system of national parks: Jasper, Banff, and Waterton Lakes. Wolverines occur throughout mainland British Columbia, except for the southern agricultural areas. Self-sustaining populations likely did not occur in the Thompson-Okanogan Highlands ecoprovince.

Wolverines occur throughout the Yukon Territory, with an estimated 4,200 south of 66° (Banci 1987) and throughout mainland Northwest Territories. They occur continuously in mainland Alaska (LeReseche and Hinman 1973) but on only some of the southeastern islands. Records from the Canadian arctic islands are spatially and temporally sporadic. Wolverines have been reported from Victoria, King William, Winter, Melville, Ellesmere, Little Cornwallis, and Baffin Islands (Manning 1943; Anderson 1946; Holbrow 1976). These sightings likely indicate occasional animals, rather than self-sustaining populations, that have wandered in search of resources.

The presettlement geographic range of wolverines extended southward from Canada through the montane ecoregions to Arizona and New Mexico (Hash 1987). However, it is not known whether these southern occurrences represent reproducing populations or dispersers. Wilson (1982) noted that wolverines at the southern edge of their distribution were limited to montane boreal regions, with conspicuous gaps in the Basin and Plains ecoprovinces. The Thompson-Okanogan Highlands and the Central Rocky Mountain Basins ecoprovinces also were gaps in the distribution, despite occasional records. The northward retreat of wolverine distribution in the United

States began in the 1840's (Hash 1987). Today wolverines occur in Montana, Idaho, Wyoming, Colorado, Washington, Oregon, and California (Appendix B).

Montana

Wolverine populations in Montana were near extinction by 1920 (Newby and Wright 1955). However, numbers increased in the western part of the state from 1950 to 1980 (Newby and McDougal 1964; Hornocker and Hash 1981). Newby and Wright (1955) and Newby and McDougal (1964) believed this increase was due to increasing numbers of wolverines dispersing from Canada and later from Glacier National Park. Reduced trapping seasons on American martens (*Martes americana*) also aided this expansion by reducing trapping activity, as did low fur prices for wolverines and for lynx (*Lynx canadensis*) (Hash 1987).

Idaho

Reports in the mid 1930's and 1940's suggested that wolverines mostly occurred in the inaccessible mountains in the center of the state (Davis 1939; Rust 1946). Records in the late 1940's came from the northern panhandle (Pengelley 1951). Nowak (1973) reported several animals taken from the central mountains, apparently reflecting a comeback. The present distribution includes mountainous areas from the South Fork of the Boise River north to the Canadian border (Groves 1988). Groves (1988) concluded that wolverine occurred mostly in the Selkirk Mountains and the Sawtooth Mountain-Smokey Mountain complex.

Wyoming

Skinner (1927) estimated the Yellowstone population at 6 or 8 and believed that it was near extinction. Newby and McDougal (1964) believed wolverine had expanded their range into the southwestern part of the state, as did Hoak et al. (1982). There are 100 records available from 1961 to 1991, all in the western third of the state (unpublished data in Maj and Garton 1992).

Colorado

Grinnell (1926) reported a few wolverines "as far south as southern Colorado in the high mountains" and wrote of three captures in the southeast and northeast parts of the state. These latter records likely were of dispersers. Armstrong (1972) listed many old records from western Colorado but could locate only one specimen. Nowak (1973) recorded a specimen from south of Denver in 1965 and mentioned other sight records. Nead et al. (1985) doubted that wolverines were historically common in Colorado and suggested that current numbers were not self-sustaining.

Washington

Scheffer (1938) concluded that the few wolverines in Washington were individuals wandering from Canada. Some records in atypical habitats indicate dispersing wolverines, such as a male that was trapped in the center of the Okanogan Valley (Scheffer 1941). After no records in the state for over 20 years, three wolverines, all adult males, were killed and another seen in central and southern counties in 1964 and 1965 (Patterson and Bowhay 1968). Johnson (1977) suggested that wolverines were present in the Cascade Range between 1890 and 1919 but absent or rare throughout the state from 1920 through 1959. He believed they expanded their range in the 1960's and 1970's by dispersal from Canada. There are 28 records for the state for the period 1970 to 1990 (unpublished data in Maj and Garton 1992); their current distribution is not known.

Oregon

Bailey (1936) reported wolverines to be rare in Oregon. Kebbe (1966) referred to unverified reports that indicated that a remnant population existed in remote areas of the Cascade Range. Patterson and Bowhay (1968) referred to an unpublished report of an adult male killed in the Cascades in 1965, the first authentic record since 1912. Yocum (1973) suggested that the species had increased in abundance since the late 1950's. There are 23 records from 1981 to 1992, compared to 57 records from 1913 to 1980 (unpublished data in Maj and Garton 1992); the current status in the state is not known.

California

The historic range of the wolverine in California included much of the Sierra Nevada ecoprovince (Grinnell et al. 1937; Schempf and White 1977). Wolverines were believed near extinction in the early 1920's (Dixon 1925; Fry 1923). Jones (1950) concluded that the species was still rare and declining. Yocum (1973, 1974) believed that wolverines were becoming established in the mountainous areas of northwestern California, from "surviving nuclei" to the north. The current range includes a broad arc from

Del Norte and Trinity counties through Siskiyou and Shasta counties, and south through the Sierra Nevada to Tulare County (Schempf and White 1977). Reports in Kovach (1981) expanded this range to include the White Mountains.

Dispersal Corridors

Wolverines in the southern part of the Pacific Northwest Coast and Mountains ecoprovince are becoming isolated from the northern portion of the ecoprovince by heavy development in British Columbia. However, occasional reports within the Thomson-Okanogan Highlands ecoprovince of British Columbia and Washington suggest that this may be a dispersal corridor. It is also possible that wolverines have become isolated within the Sierra Nevada ecoprovince of California because of human activities.

Wolverines in the Colorado Rocky Mountains ecoprovince are isolated from areas to the north by the Central Rocky Mountain and Wyoming Basins (unpublished data in Maj and Garton 1992). These basins are arid and have been altered by human land uses. Geographic isolation of wolverines may seem unlikely because of their extensive movements. However, whether animals moving long distances successfully complete dispersal and reproduce is not known. Ecotypic variation over the geographic ranges of other large carnivores has been shown with DNA analyses (Fain in press; Knudsen and Allendorf in press) but is poorly known for the wolverine.

Taxonomy and Morphological Variability

Most authorities consider all wolverines in North America and Eurasia to belong to a single species (*Gulo gulo*) (Ognev 1935; Anderson 1946; Rausch 1953; Kurten and Rausch 1959; Krott 1960; Corbet 1966). Subspecific designations have been recognized to varying degrees. Hall and Kelson (1959) recognized *G. gulo katschemakensis* from the Kenai Peninsula, Alaska, but Dagg and Campbell (unpublished data 1974) considered this subspecies invalid. The Pacific wolverine, *G. gulo luteus*, was first described by Elliot (1903) from California and Grinnell et al. (1937) recognized this as a southern subspecies on the basis of skull characteristics alone. Further evidence to support a subspecific classification for the Pacific wolverine has not emerged. In an evaluation of the status of *G. gulo vancouverensis*, skulls of the Vancouver island wolverine (Banci 1982) differed in size and shape from those on the British Columbian mainland, although the comparison was based on a small sample. However, these mainland wolverines also differed from those in the Yukon, two populations that likely interbreed. Further, ecotypic variation was reflected in at least three regional mainland populations (Banci 1982).

Variation in body size of wolverines suggests ecotypic variation. Adult females in the Southern Arctic ecoprovince are the largest (K. Poole, pers. comm.). The smallest adult females occur in the Northern Rocky Mountain Forest, the Pacific Northwest Coast and Mountains, and the Shining Mountains ecoprovinces. In general, the most sexually dimorphic wolverines occur in the south and the least in the north. These results are consistent with those of Banci (1982), who found that skull measurements that differentiated among geographic areas differed by sex.

Management Considerations

1. Wolverines were widespread but likely occurred at low densities in the western conterminous United States in presettlement times. Areas that supported reproduction then are not known.

2. Wolverines are difficult to observe, even where they are relatively abundant. Frequency of sightings may not reflect population size but can result from greater human access to wolverine range. Wolverines can travel long distances and sightings may not indicate reproducing populations. Conversely, a lack of sightings does not mean a lack of presence. The presence or absence of wolverines needs to be confirmed in the field with the use of remote cameras or confirmations of tracks if information on their presence is important to managers.

3. Wolverines occupying different ecoprovinces differ in body size and behavior. This variation may represent local adaptation and may have important conservation implications.

Research Needs

1. Determine genetic diversity among wolverine populations. This information will assist in recovery programs.

2. Determine whether wolverine populations in the conterminous United States are self-sustaining or dependent on emigration from Canada.

POPULATION ECOLOGY

Reproduction and Natality

Wolverines exhibit delayed implantation, during which development of the embryo is arrested at the blastocyst stage. Implantation in the uterine wall can occur as early as November (Banci and Harestad 1988) or as late as March (Rausch and Pearson 1972). Because active gestation lasts 30-40 days (Rausch and Pearson 1972), birth can therefore occur as early as January or as late as April (Banci and Harestad 1988). For many mammals, winter may be an inhospitable time to give birth. However, ungulate carrion may be more plentiful in winter, which may favor parturition at that time in wolverines. Parturition in Norway was shown to correspond closely with the period when reindeer were most vulnerable (Haglund 1966; Roskaft 1990). Security cover for kits may also be enhanced during winter; snow tunnels or snow caves are characteristic natal and maternal dens for wolverine in many areas.

Females do not breed their first summer (Rausch and Pearson 1972; Liskop et al. 1981; Magoun 1985; Banci and Harestad 1988) and authors have reported varying proportions of the subadult age class (1-2 years) that breed. Banci and Harestad (1988) reported 7% in the Yukon, contrasting with the 50% reported by Rausch and Pearson (1972) in Alaska and the Yukon, and 85% reported by Liskop et al. (1981) for British Columbia. Differences in how wolverine ages were classed make comparisons among studies difficult; the subadult age class in the latter two studies may have included adults. Most males are sexually immature until 2+ years of age (Rausch and Pearson 1972; Banci and Harestad 1988). Testis weights increase throughout the winter (Rausch and Pearson 1972; Liskop et al. 1981; Banci and Harestad 1988) and by March, all adult males are in breeding condition (Liskop et al. 1981). Rausch and Pearson (1972) reported a peak in testis weights in June, presumably indicating the peak in breeding activity.

Reproductive Rates

Increasing litter sizes with age are important factors in productivity (Banci and Harestad 1988), as is common for mammals (Caughley 1977). For the Yukon, mean numbers of corpora lutea per female ranged from 3.1 for 2- to 3-year-old animals to 4.4 for those older than 6 years (Banci and Harestad 1988). Numbers of corpora lutea overestimated numbers of fetuses, whereas numbers of placental scars did not differ from those of fetuses (Band and Harestad 1988). Litter sizes as large as six in captive animals (Rausch and Pearson 1972) and four in wild ones have been reported. Litter size after den abandonment is typically fewer than three (Pulliainen 1968; Magoun 1985).

The proportion of adult female carcasses that were pregnant was 74% in the Yukon (Band and Harestad 1988), less than the 92% found in Alaska and the Yukon (Rausch and Pearson 1972) and 88% in British Columbia (Liskop et al. 1981). In the Yukon, the proportion of females that were pregnant in age classes 2-3 to 5-6 years ranged from 92% to 53%, respectively, but was 37% for females older than 6 years. Older females may be capable of larger litters, but fewer females in these older age classes may produce litters. In northwest Alaska, during a year when food was scarce because caribou were uncommon, none of four collared adult females were known to have produced young (Magoun 1985). In the 13 collective years of sexual maturity during which 6 adult females were observed, young were produced in only 5 years of wolverine life (Magoun 1985). In Montana, an adult female produced no young in the 3 years she was observed and only 50% of adult females were thought to be pregnant in any year of the 5-year study (Hornocker and Hash 1981). Two of 3 adult females in southwest Yukon did not reproduce young over the 3 years of that study (Band 1987).

The incidence of nonpregnant females appears to be related to nutritional status and the demands of lactation. Kits are weaned at 9-10 weeks (Krott 1960; Iversen 1972). The basal metabolic rate of wolverines during these first months of life increases in proportion to body weight raised to the 1.41 power ($W^{1.41}$) (Iversen 1972), higher than reported for other mammals where total heat production prior to weaning increases in proportion to body weight ($W^{1.0}$). Iversen (1972) suggested that the rapid increase in total heat production during the early phase of growth resulted from a faster growth of the high energy-producing tissues compared to other mammals. Young wolverines grow quickly after weaning and by 7 months of age have achieved adult size (Magoun 1985). The rapid growth of kits before and after weaning presumably places high energetic demands on mothers and can affect female reproduction in the immediate future (Band 1987).

Adult females appear to breed, but not necessarily whelp, yearly (Magoun 1985). Loss of young likely

occurs early in active pregnancy (Banci and Harestad 1988). The condition of females before implantation may be the most critical factor determining successful birth, but not survival of young. Although sample sizes were small (n = 5), Magoun (1985) observed some neonatal (preweaning) mortality.

Sampling Problems and Population Characteristics

Estimates of age and sex composition of wild populations have suffered from small sample sizes. The sex ratio is generally 1:1 (table 2). Sex ratios biased toward males were observed in northern Yukon and southcentral Alaska, where it was suspected that the capturing method, darting from helicopters during March, excluded denning females (D. Cooley, pers. comm.; Magoun 1985). The exclusion of females in a sample will also bias age ratios toward adults because young females exhibit a fidelity to the natal area that young males do not (Magoun 1985). The proportion of captured wolverines that were adults in northern Yukon and southcentral Alaska studies, 76% and 86%, respectively, were the highest of all studies (table 2).

Only studies in Idaho (unpublished data in Copeland 1993), southwest Yukon (Banci 1987), northwest Alaska (Magoun 1985), and Montana (Hornocker and Hash 1981) likely reflect the true demography of residents. The results of these studies were similar. The sex ratio was close to 1:1 in all studies. The proportion of adults ranged from 68% to 73%. More subadults occurred in northwest Alaska; however, subadult and young-of-the-year age classes were based on small samples in all studies. The proportion of juvenile wolverines, especially males, is likely to be the most variable among studies of unexploited wolverine populations. The longer a study and the more effort placed into tagging and following juveniles, the greater the accuracy in estimating the proportion of the population in this age class prior to dispersal.

Collecting information on transients is inherently difficult. Males disperse as young of the year or as subadults (Gardner 1985; Banci 1987), or at 2 years of age (Gardner 1985). Female offspring tend to remain close to their mother's home range (Magoun 1985), although some also disperse. Thus, the transient segment of the wolverine population is most likely composed, in decreasing proportions, of juvenile males, juvenile females, and adult males. The proportion of wolverines that are transient in any year varies with kit production, survival of neonates, and mortality. This transient segment likely plays an important role in maintaining the distribution and population characteristics of wolverines.

Estimates of wolverine densities are difficult to compare among studies because of inconsistent methods. However, two techniques show promise: (1) where aerial surveys are feasible, estimation based on probability sampling (unpublished data in Becker and Gardner 1992) and (2) in forested areas, remote cameras at bait stations (unpublished data in Copeland 1993). Because unique markings often allow the individual identification of wolverines, the latter has promise for mark-recapture as well as for detection.

Natural Mortality

Wolverines have few natural predators but are occasionally attacked and killed, but seldom eaten, by

Table 2.-Sex and age composition of resident wolverine in telemetry studies in North America, excluding dependent kits.

Location	Sex Ratio M:F	(*n*)	% Young of year	% Subadult	% Adult[1]	*n*	Reference
SW Yukon	1.0:1	(5:5)	20% (3)	7% (1)	73% (11)	15	Banci 1987[2]
NW Alaska	0.8:1	(10:12)	17% (3)	17% (3)	68% (13)	19	Magoun 1985[3]
NW Montana	0.9:1	(11:13)		29% (7)	71% (17)	24	Hornocker and Hash 1981[4]
N Yukon	2.5:1	(10:4)	(1) 7%	7% (1)	86% (12)	14	D. Cooley, pers. comm.
SC Alaska	2.4:1	(12:5)		24% (4)	76% (13)	17	Whitman and Ballard 1983[5]
NC Idaho	1.2:1	(6:5)	0%	27% (3)	73% (8)	11	Copeland 1993, unpubl.

[1] *Young-of-the-year 0-1 years, subadult 1-2 years, adult 2+ years.*
[2] *Including 5 unmarked residents.*
[3] *Sex ratio includes 2 wolverine of unknown age.*
[4] *Subodult age group not differentiated into yearling and subadult. Method of aging not indicated; likely visual inspection and not cementum analysis.*
[5] *Ages based on subjective estimate of tooth wear; one unknown male classed as adult because of large weight, 17.7 kg. This study is a continuation of Gardner 1985.*

wolves and other large carnivores (table 3, Burkholder 1962; Boles 1977; unpublished data in Gill 1978; Banci 1987). Hornocker and Hash (1981) described injuries they believed had been inflicted by a cougar (*Felis concolor*) and suggested that bears and eagles could kill wolverines, especially kits. The importance of predation on wolverine kits has not been documented. Wolverine mothers go to great lengths to find secure dens for their young, suggesting that predation may be important. Although not documented, adult males may kill kits. Magoun (1985) observed males visiting females with young prior to breeding, and on one occasion a male occupied the natal den of a female and her kit. Assuming that the turnover of resident males were high, a male would increase his fitness by killing kits that he likely did not sire. He would not only be killing another male's progeny, but be increasing the possibility that the female would successfully raise his kits the next year. This is because the death of her kits would improve her physiological condition through the early cessation of lactation.

Some wolverines, especially males, may be killed by conspecifics. Males in northwest Alaska had fresh wounds on their heads when captured in April, suggesting that the approach of the breeding season increases aggressive behavior (Magoun 1985). Altercations between young males and adult males may be the proximate encouragement for the former to disperse (Banci 1987).

Starvation likely is an important mortality factor for young and very old wolverines. Suspected deaths from starvation include two young-of-the-year females in southwest Yukon (Banci 1987) and a young female and an old male in Montana (Hornocker and Hash 1981). These animals relied heavily on baits just before their deaths, suggesting that very young and old age classes may be unsuccessful foragers, even if food is abundant (Hornocker and Hash 1981; Banci 1987). Documenting the fates of young males is difficult because of their extensive movements and it is not possible to predict whether sexes differ in their susceptibility to starvation.

The age-specific mortality reported in studies of collared wolverines (table 3) was 57% for adults, 7% for subadults, and 36% for young of the year. However, the mortality rates of juvenile wolverines are underestimated in these studies. The long distances covered by young of the year and subadults, especially males, makes it difficult to ascertain their fates unless they are trapped and their deaths reported. Mortality in these young age classes likely is substantial. Transients likely have a higher mortality rate than residents because they do not benefit from hunting in familiar home ranges. So, they likely have a greater chance of starvation, of being killed by conspecifics and of encountering traps. Krott (1982) believed that one-third to one-half of subadult wolverines perished during dispersal.

Table 3.--Fates of radio-collared wolverine.

			Cause of mortality							
Location	**n**	**Years studied**	**Harvest**	**Starvation**	**Predation**	**Other**	**Unknown**	**Total**	**Annual %**	**Reference**
NW Alaska	24	5	3					3	2.5	Magoun 1985
SC Alaska	16	3	2				1	3	6.2[1]	Whitman & Ballard 1983
SW Yukon	10	3	2	2	1	1		6	20.0[2]	Banci 1985
NW Montana	24	5	5	2		1		8	6.7[3]	Hornocker & Hash 1981
NC Idaho	11	1			1		1	2	18.1[4]	Copeland 1993, unpubl.
Total	86		12	4	2	2	2	22	10.6[5]	
% of total mortality			54%	18%	9%	9%	9%			

[1] *Status of 12 of the 16 wolverine unknown, 1 capture mortality not included.*
[2] *"Predator" = wolf; "other" = parasitic pneumonia, a female believed to be nutritionally stressed after raising young.*
[3] *"Other" = old female, suppurative metritis, uterus was badly infected; an additional 10 mortalities of unmarked wolverine occurred during the study, all from trapping.*
[4] *Two kits not included, one of which died from a capture-related cause; "predator" unknown; other = "old" female wolverine that had become habituated to trap bait; status of 1 male unknown.*
[5] *Mean of 5 annual mortality rates; harvest mortality represents an annual mean of 5.3% and natural mortality, 5.3%.*

Trapping Mortality

Over most of its distribution, the primary mortality factor for the wolverines is trapping (trapping and hunting mortality are considered together in this section). In telemetry studies, trapping has accounted for over half of all mortalities, although only two of the five study populations were trapped and the Montana study area was only trapped for the first 2 years of the 5-year study (table 3, Hornocker and Hash 1981). Most of these deaths were of animals that left the nonharvested study areas.

The cumulative impacts of trapping, habitat alterations, forest harvesting, and forest access on wolverines are not understood. Trapping can have important implications for conservation. Ensuring that a recovering population is protected from trapping must be accompanied by monitoring of trapping impacts on potential dispersers from surrounding populations.

Harvest data can provide insights into the vulnerability of age and sex classes. However, without information on the proportion of the population being harvested, on natural mortality, and on the additive or compensatory nature of trapping mortality, little can be said about the sustainability of such harvests. Harvests of juvenile wolverines, especially early in the season, likely are compensatory because of their suspected high natural mortality. Some harvests of adults, those that are nutritionally stressed, also will be compensatory. But, in general, I believe that the harvest of most adults is additive to natural mortality.

In one of the few attempts to estimate the sustainability of wolverine harvests, Gardner et al. (unpublished data 1993) used demographic data from radio-telemetry studies in Alaska and the Yukon (Banci 1987; Gardner 1985; Magoun 1985) in conjunction with density estimates (unpublished data in Becker and Gardner 1992) and harvest sex-age compositions (Gardner 1985; Banci 1987) to construct a population model. The annual sustainable harvest was an estimated 7-8% of the fall population. Recent wolverine harvests in parts of Alaska have exceeded 10% (unpublished data in Gardner et al. 1993).

Density and Population Trends

In general, wolverine densities are low relative to carnivores of similar size, although there can be a tremendous range, from 40 km^2 to 800 km^2 per wolverine (table 4). Annual trapper questionnaires have been used in the Yukon, British Columbia, and Alberta to determine furbearer population trends and factors responsible for changes in population status (B. Slough, pers. comm.; unpublished data in Rollins 1993; unpublished data in McFetridge 1993-1991). These surveys have indicated that over the past 4 years, wolverine populations have decreased in the Boreal Uplands, Sub-Boreal Interior, Central British Columbia Plateaus, Thompson-Okanogan Highlands, and Shining Mountains ecoprovinces, despite a general decrease in trapper effort. These ecoprovinces are characterized by extensive forest harvesting, as well as oil and gas exploration in the Boreal Uplands, ranching in the Central British Columbia Plateaus, and increasing human settlement and roadbuilding, especially in southern Canada.

Population Management Strategies

Refugia, large areas that are not trapped and free from land-use impacts, can serve as sources of dispersing individuals and have been shown to be effective at ensuring the persistence and recovery of fisher and American marten populations (deVos 1951; Coulter 1960). The persistence of wolverine populations in Montana, despite years of unlimited trapping and hunting, was attributed solely to the presence of designated wilderness and remote, inaccessible habitat (Hornocker and Hash 1981). Wolverines persisted in southwestern Alberta despite their extirpation elsewhere in the province, largely because of the presence of large refugia in the form of national parks.

Management Considerations

1. Wolverines occur at low densities, even under the most optimal conditions where they have been studied. This makes detection of wolverines and determination of the effects of management activites on them difficult.

2. Reproductive rates are low and sexual maturity delayed, even in comparison with other mammalian carnivores.

3. Trapping accounts for a high proportion of wolverine mortality, affecting even populations that are locally protected.

4. Transient wolverines likely play a key role in the maintenance of spatial organization and the colonization of vacant habitat. Factors that affect movements by transients may be important to population and distributional dynamics.

5. If an objective is to have wolverines colonize an area through dispersal, then trapping of the source

Table 4.--Estimated densities of wolverine populations in North America, by location. Densities are expressed as a range when more than one estimate was available.

Density (km^2/wolverine)	Location	Method of calculation	Reference
North Slope of Alaska			
48-139[1]	NW Alaska	Telemetry, mean home range size	Magoun 1985
Central Yukon			
409-778	NC Yukon	Habitat suitability rating[2]	Banci 1987
Northern Boreal Forest (Yukon and British Columbia)			
37-656	SC Yukon	Habitat suitability rating[2]	Band 1987
177	SW Yukon	Telemetry, mean home range size	
Alaska Range			
209	SC Alaska	Logarithmic extrapolation[3]	Whitman and Ballard 1983
185, 213	SC Alaska	Aerial estimator[4]	Becker and Gardner 1992
Taiga Plains of Northwest Territory			
210	NE British Columbia	Harvests, Snow-tracking	Quick 1953
Northern Rocky Mountain Forest			
65[5]	NW Montana	Telemetry, mean home range size, snow-tracking	Hornocker and Hash 1981
150-200	NW Montana	Estimated, fringe areas to core study area	Hash 1987

[1] *Resident fall population, including adults, sub-adult daughters that settled next to natal area, and kits.*
[2] *Density for one ecoregion determined from an intensive field study. Habitat capability of other ecoregions extrapolated from relationship between trapper success and density.*
[3] *Includes kits but not sub-adults; assumes that male home ranges average 627 km^2.*
[4] *Furbearer estimation technique based on probability sampling (Becker and Gardner 1992).*
[5] *May have included juveniles.*

population, even if it is some distance away, may interfere with this objective. Because wolverines are wide-ranging, conservation programs need to transcend jurisdictional boundaries.

6. Harvest data can be used to monitor wolverine populations.

7. Refugia may be the best means of ensuring persistence of wolverine populations. Because wolverines are wide-ranging, refugia must be very large. Areas assigned permanently to one trapper can serve as refugia when pelt prices and trapping effort are low, which is the current situation in most of western North America. However, for refuges to be effective in population maintenance, they must not be harvested regardless of pelt prices.

Research Needs

1. Investigate the proportion of females that are pregnant in the wild, the proportion of kits that survive to weaning, and the factors that limit reproductive success. Knowing how reproductive success varies with environmental factors such as food availability, female condition, and the availability of natal dens will help in predicting population growth rates.

2. Use population models to understand the dynamics of wolverine populations and to determine the sustainability of harvests. Field studies are needed to increase the data base on population attributes and to parameterize these models. Mathematical modeling can also help to direct future research.

3. Invesigate the utility of remote cameras as a means of detecting wolverines or indexing their numbers.

4. Determine the cumulative impacts of trapping and timber harvesting on wolverine populations.

REPRODUCTIVE BIOLOGY

Mating Behavior

Wolverines have bred in captivity during May (Mehrer 1976) and July (Mohr 1938) and in the wild during June (Krott and Gardner 1985) and August

(Magoun and Valkenburg 1983). All adults, even females with dependent kits, appear to breed. Females may take longer to become estrous in their first breeding season and females that are not raising kits may come into breeding condition earlier than females with kits (Magoun 1985). The implication of a staggered entry into estrus by females is that males, which must travel extensively to monitor the breeding condition of females, have a better chance of encountering estrous females than if all females were in estrus synchronously. A long breeding season and prolonged estrus improve these chances further.

Breeding of wolverines in the wild in Alaska was described by Magoun and Valkenburg (1983) and Krott and Gardner (1985). Breeding pairs of wolverines restrict their movements and stay together, usually within a few meters, for 2-3 days (Magoun and Valkenburg 1983), suggesting that they copulate repeatedly. Induced ovulation has been shown for other mustelids and likely also occurs in the wolverine, necessitating prolonged intromission.

Natal Dens

Information on the use of natal dens in which the kits are born by wolverines in North America is biased to tundra regions where dens are easily located and observed. These natal dens typically consist of snow tunnels up to 60 m in length (Pulliainen 1968; Magoun 1985; Roskaft 1990). Bedding does not appear necessary, inasmuch as kits were found in shallow pits dug on the ground (Pulliainen 1968). Snow tunnels in northwest Alaska were also used by lone wolverines (Magoun 1985), suggesting that they dig tunnels or use existing tunnels as resting sites as well.

Natal dens above treeline appear to require snow 1-3 m deep (Pulliainen 1968) that persists into spring. In Finland, Pulliainen (1968) believed that dens that wolverine had dug themselves were preferred, because caves were rarely used, although available. Little is known of the distribution of den sites in the landscape. The proximity of rocky areas, such as talus slopes or boulder fields, for use as dens or rendezvous sites was important for wolverines in Norway (Roskaft 1990), in the Soviet Union (Ognev 1935), and in Idaho (unpublished data in Copeland 1993). Natal dens may be located near abundant food, such as cached carcasses or live prey (Haglund 1966; Rausch and Pearson 1972; Youngman 1975).

Females with young in Arctic Alaska spend much of their time in natal dens during March and April (Magoun 1985). Dens are abandoned in late April or early May, because of snowmelt (Magoun 1985; Pulliainen 1968). While the kits are too young to travel, the female hunts alone after leaving the kits at rendezvous sites (Magoun 1985). These rendezvous sites usually were portions of snow tunnels remaining from winter or remnant snowdrifts (Magoun 1985). Two other rendezvous sites included a rock cave and a boulder-strewn hilltop with no large snowdrifts (Magoun 1985).

Limited information is available on dens in forested habitat. In northern Lapland, most of the dens in forests were associated with spruce (*Picea* sp.) trees; five consisted of holes dug under fallen spruces, two were in standing spruces, and one natal den was inside a decayed, hollow spruce (Pulliainen 1968). Ognev (1935) reported that dens in Kamchatka were usually constructed in the "hollows" (cavities) of large trees. Rarely, kits have been found relatively unprotected, on branches and on the bare ground (Myrberget 1968). If females are disturbed they will move their kits, often to what appear to be unsuitable den sites (Pulliainen 1968).

Pulliainen (1968) hypothesized that one of the factors affecting the selection of a natal den site was the ease with which it could be adapted to a den. Seton (1929) reported dens in abandoned beaver lodges (as did Rausch and Pearson 1972), old bear dens, creek beds, under fallen logs, under the roots of upturned trees, or among boulders and rock ledges. In Siberia, dens were found in caves, under boulders and tree roots, and in accumulations of woody debris consisting of broken or rotted logs and dry twigs (Stroganov 1969). Natal dens in Montana were most commonly associated with snow-covered tree roots, log jams, or rocks and boulders (Hash 1987).

Management Considerations

1. Where wolverines occupy alpine areas in summer, the impact of human recreation on mating pairs and on family groups needs to be considered. Regulations that maintain the wilderness quality of an area, such as management of access, will help to minimize possible impacts on breeding wolverines and on females with kits.

2. Den sites in forested areas described to date in forested areas suggest that physical structure may be important for denning. Low availabilty of natal dens may limit reproduction in some areas, especially

those that have been extensively modified by logging or other land-use practices.

3. The distribution of natal den and rendezvous sites in the landscape, with respect to the distribution of food sources and security cover, may impact kit survival. In tundra habitats, deep snow drifts, such as in ravines, appear to be important.

4. Habitats that provide the appropriate structures, such as large cavities, coarse woody debris, and old beaver lodges, likely will provide den sites. Information is not available on the numbers of natal or maternal dens or rendezvous sites required.

Research Needs

1. Investigate factors important in the selection of natal and maternal dens, especially in forested habitats. Determine how the structure and distribution of natal dens and rendezvous sites contribute to kit survival.

2. Determine how the distribution and abundance of predators such as cougars, bears, and raptors affect the location and types of natal dens and rendezvous sites used by wolverines.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

Wolverines are generally described as opportunistic omnivores in summer and primarily scavengers in winter. Winter diets have been determined from gut contents and scats and mostly reflect northern areas: the Yukon, Alaska, and the Northwest Territories. In the southern part of the wolverine's geographic range, quantitative diet data are available only for Montana.

Diets

The frequency of occurrence of prey remains does not necessarily indicate importance, because the size of prey and the amounts consumed affect their appearance in scats and gastro-intestinal tracts. Also, scavenging species tend to feed on animal remains, which tend to be bones and fur. This can overestimate the importance of scavenged foods relative to animals (e.g., snowshoe hare [*Lepus americanus*]) consumed in their entirety. Still, scats and gastrointestinal tract contents likely reflect annual and seasonal differences in food availability.

All studies have shown the paramount importance of large mammal carrion (table 5), and the availability of large mammals underlies the distribution, survival, and reproductive success of wolverines. Over most of their range, ungulates provide this carrion, although in coastal areas, marine mammals may be used. Wolverines are too large to survive on only small prey.

Large mammals are important all year (table 5), although carrion tends to be more available at some seasons than others. Ungulate carrion from natural mortalities and kills by humans is most available in fall and winter. For barren-ground caribou, adults dying during migration and calves dying at or just after birth become available in spring. In the coastal Arctic in the spring, wolverines prey on seal pups on sea ice (Anne Gunn, pers. comm.) and in some coastal Alaskan areas, sea mammal carcasses provide abundant carrion (LeReseche and Hinman 1973).

North of the boreal forest, barren-ground caribou are the most important source of ungulate carrion (table 5). Novikov (1956) thought some Old World wolverines migrated to follow reindeer (*Rangifer rangifer*), their primary winter food. Such a migration was also hypothesized by Kelsall (1981) for Canada because of the numbers of wolverine taken during predator control on occupied caribou ranges in winter (Kelsall 1968). Research has not shown wolverines to migrate, although they associate closely with caribou in the North. Moose are consumed where available (Kelsall 1981). The distribution of wolverines in northern Saskatchewan has closely followed the changes in distribution of the barren-ground caribou (W. Runge, pers. comm.). This may also be true in Alberta and Manitoba. The decline of the wolverine in Labrador coincided with the decline of caribou (Banfield and Tener 1958) and recent sightings of wolverines in Labrador have coincided with expansions of caribou range (Banci 1987).

South of the tundra, ungulates gain importance according to their availability. In the Yukon Forest and Northern Boreal Forest ecoprovinces of central Alaska and the Yukon, both moose and caribou are common (table 5). Where they occur, Dall sheep (*Ovis dalli*) and mountain goat (*Oreamnos americanus*) are eaten, but less so than moose or caribou, perhaps because the precipitous terrain occupied by sheep and goats reduce their accessibility (Banci 1987). Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) were the primary ungulates in the diet of wolverines in Montana (table 5, Hornocker and Hash 1981).

Bone and hide may be important foods. They may be available for several months after an ungulate dies (Haynes 1982). Wolverines in northwest Alaska and in the Yukon at times consumed only bone (Magoun 1985; Banci 1987). The presence of bone and fur in the diet (table 5) emphasizes the use that wolverine make of old kill sites, and the general scarcity of food. The large numbers of wolverines with empty gastro-intestinal tracts in food habits studies (table 5) is evidence of the uncertainty in the availability of food.

Table 5.-Diets of wolverine in North American ecoprovinces.

	Percent frequency of occurrence[1]						
Prey Item	**Northern Boreal Forest (Yukon & British Columbia)**	**North Slope of Alaska**	**Central Alaska**			**Northern Territories**	**Northwest Rocky Mountains**
Winter							
Snowshoe hare	27		6	[2]	45	13	16
Porcupine	16		3	15		2	4
Sciuridae	14	40	9			2	11
Aves	12	11	11	[2]	6	12	6
Small mammals	10	30	20	[2]	16	2	6
Beaver/muskrat	<1			3		4	2
Carrion							
caribou	8	37	20	60[3]		53	80
moose	14		25			33	3
other	7[4]						27[5]
unidentified	23			6			45[5]
fat/flesh	16				12		
bone	32						
Fish	5				6	14	
Other	4	18	20		2	5	18
Empty/trap debris	31				73	39	
Reference[7]	a)	b)	c)	d)	e)	f)	g)
Snow-Free Periods							
Ungulate	7, 30[8]	12[8]	33[9]				
Ground squirrel	0, 17	40	33				
Aves[10]	7, 14	2	11				
Mice & voles[11]	93, 57	12	11				
Beaver			11				
Marmot	7, 0						
Reference[12]	a), b)	c)	d)				

[1] Percent frequency Is based on the occurrence of each prey of the total number of scats or gastro-intestinal (g.i.) tracts. Empty g.i. tracts were not used In calculations of percent occurrence for prey items.
[2] Proportion not reported but rare,
[3] Undifferentiated between moose and caribou.
[4] Bovids.
[5] Deer or elk.
[6] Domestic cow and horse.
[7] a) Banci 1987, Yukon; n=411 gastro-intestinal tracts. November-March, 1982/83-1984/85. 126 g.i. tracts were empty or contained only vegetation or only wolverine hair.
b) Magoun 1985, Alaska; n=82 scats, November, February, March, 1979-1980.
c) Gardner 1985, Alaska; n= 35 colons only, December-March 1979-1982.
d) Rausch 1959, Alaska; n=20 stomachs.
e) Rausch and Pearson 1972, Alaska; n=192 gastro-intestinal tracts, winter. Only 51 g.i. tracts with prey items.
f) Poole 1991-1992, Northwest Territories; n=173 stomachs, winter 1987/88-1991/1992.
g) Hornocker and Hash 1981, Montana; n= 56 scats, 5 winters December 1972 April 1977.
[8] Caribou.
[9] Moose.
[10] North Slope; ptarmigan.
[11] Microtus sp., Lemmus sp., Phenacomys sp., Clethrionomys sp.
[12] a) Newell 1978; 15 scats collected on trails,
b) Newell 1978; 30 kit scats collected from 2 natal dens.
c) Magoun 1985; n=48 observations of 362 5-minute observation periods, May-August, 1978-1981.
d) Gardner 1985; n=9 aerial observations; April-mid-October, during 70 telemetry flights, 1980-1982.

Small mammals are primary prey only when carrion of larger mammals is unavailable (Banci 1987).

Snowshoe hares, at both high and low population levels, were important in the diets of wolverines in the Yukon (Banci 1987, table 5) and Alaska (Rausch and Pearson 1972). I expect that, especially during hare population lows, habitats that maintain pockets of them (Hatler 1988) will be important foraging areas for wolverines. In western North America, there is a general decrease in abundance and in the amplitude of population fluctuations of snowshoe hares with decreasing latitude (Hatler 1988). Hares likely are less important in the wolverine diet in these areas.

Porcupines (*Erethizon dorsatum*) occur in wolverine diets in Alaska, the Yukon, and Montana (table 5). Although they represent a large meal, porcupines appear to be limited to those wolverines that have learned to kill them (Banci 1987). The frequency of red squirrels (*Tamiasciuris hudsonicus*) in wolverine diets in northern forested habitats (Gardner 1985; Banci 1987) is a reflection of their wide distribution and availability throughout winter. Arctic ground squirrels (*Spermophilus parryi*) composed 26% of all sciurids in the winter diet of Yukon wolverines (Banci 1987) and the majority of the diet in northwest Alaska, where snowshoe hares were absent (Magoun 1985). Wolverines cache hibernating sciurids such as ground squirrels and hoary marmots (*Marmota caligata*) in the snow-free months for later use and excavate them from winter burrows (Gardner 1985; Magoun 1985).

Birds occur in the diet according to their availability. Wolverine prey on ptarmigan (*Lagopus* spp.) in winter in the Yukon (Banci 1987), Alaska (Gardner 1985; Magoun 1985), and the Northwest Territories (Boles 1977). Prey that occur sporadically in diets, such as American marten, weasel (*Mustela* spp.), mink (*M. vison*), lynx, and beaver (*Castor canadensis*), likely are mostly scavenged. Vegetation is consumed incidentally although ungulate rumens and may contain nutrients that wolverines cannot obtain from other foods (Banci 1987).

Some foods may be abundant and predictable--for example, spawned salmon frozen in river ice (Banci 1987). Other abundant food sources likely include spawning salmon in the fall and intertidal areas of the Pacific coast. Such areas may support high densities of wolverines (Banci 1987).

Seasonal Variation in Diets

Although data are limited, in general, diets during snow-free periods are more varied than in winter because of the greater availability and diversity of foods, such as berries, small mammals, sciurids, and insect larvae (table 5). Berries can be important in fall (Bausch and Pearson 1972) and during late winter and spring. Wolverine in southwest Yukon ate kinnikinnick (*Arctostaphylos uva-ursi*) berries that were high in carbohydrates because of freezing and thawing (Banci 1987).

Spring and summer may be the only seasons when sexual differences in diet may occur. The movements of females with kits are restricted at these times and their diets may differ from males that are not so restricted. Diet does not appear to differ by age, at least in winter (Banci 1987). Success at foraging may differ between juveniles and adults because of differences in experience, but this has not been shown.

Foraging Behavior

Although mostly scavengers, wolverines can prey on ungulates under some conditions. Because of their low foot loads (pressure applied to substrate) of 22 g/cm^2 (Knorre 1959), wolverines can prey on larger mammals in deep snow and when ungulates are vulnerable. Grinnell (1920, 1926) described wolverines killing moose, caribou, and elk. Guiget (1951) described an unsuccessful attack of a wolverine on a mountain goat and Burkholder (1962) a successful attack on a caribou bull. Gill (unpublished data 1978) described a wolverine killing a young female Dall sheep hindered by snow in the Northwest Territories. Teplov (1955) described instances in which pregnant cow moose aborted when chased by wolverines and the wolverines ate the aborted fetuses. A similar case with a wolverine and a caribou cow was observed in the Yukon (P. Temple, pers. comm.).

Caching of food by wolverines has been described by most studies except that in Montana. The frequency of caching by wolverines may be affected in various ways by the presence of other carnivores (Hornocker and Hash 1981; Magoun 1985).

Management Considerations

1. Activities that increase availability of foods generally will affect wolverines positively, whereas those that reduce prey populations will do so negatively. The close relationship between wolverines and large mammals implies that activities that decrease large mammal populations will negatively impact wolver-

ine. These activities could include wolf predation, excessive harvesting by humans and human-caused losses of ungulate winter ranges. Some ungulate species may be enhanced by the provision of early seral stages through logging or burning. However, these and other land-use activities may exclude wolverines from areas that ungulates still use if these habitats do not provide for the wolverine's other life needs.

2. Because young wolverines mature rapidly, the availability and distribution of food during the snow-free season may determine the survival of females with kits.

Research Needs

1. Investigate wolverine diets in the southern part of the geographic range. This will improve understanding of the variation in diets over the geographic range and of the importance of foraging habitats.

2. Investigate and compare diets of females with kits to lone females and males.

3. Study caching behavior by wolverine. If the types of caches used are a function of habitat type, they may be impacted by land-use activities and their absence may negatively impact wolverine survival.

HABITAT RELATIONSHIPS

Broadly, wolverines are restricted to boreal forests, tundra, and western mountains. The vegetation zones (Crowley 1967; Rowe 1972; Hunt 1974; Bailey 1980; Allen 1987) occupied by wolverines include the Arctic Tundra, Subarctic-Alpine Tundra, Boreal Forest, Northeast Mixed Forest, Redwood Forest, and Coniferous Forest. They are absent from all other vegetation zones, including the prairie, deciduous, and mixed forests of eastern North America; California grassland-chaparral; and sagebrush and creosote scrublands.

Researchers have generally agreed that wolverine "habitat is probably best defined in terms of adequate year-round food supplies in large, sparsely inhabited wilderness areas, rather than in terms of particular types of topography or plant associations" (Kelsall 1981). Although this is generally true at the landscape scale, stand-level habitat use by wolverines in forests has not been adequately investigated. Results from northern studies (Gardner 1985; Banci 1987) cannot be extrapolated to the southern part of the range, nor can the one study in the Northern Rocky Mountain Forest of Montana (Hornocker and Hash 1981) be considered representative of that ecoprovince.

Habitat Use

Landscape scale

In British Columbia, the highest harvests of wolverines per unit area and effort occur in the Shining Mountains and Northern Boreal Forest ecoprovinces. The combination of very wet mountains and very dry rainshadow valleys provides the Shining Mountains with a high diversity and abundance of large mammals, including mountain goats, mule and white-tailed deer, elk, bighorn sheep (*Ovis canadensis*), and woodland caribou (Demarchi et al. 1990). Predators such as grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolves, and cougars also are common, at least in the Canadian part of the ecoprovince. The best habitat for wolverines in the Yukon (Banci 1987) is in the Northern Boreal Forest. This ecoprovince is characterized by mountains and plateaus separated by wide valleys and lowlands, with extensive subalpine and alpine habitats (Demarchi et al. 1990). Ungulates and predators are abundant here as well.

I expect that the lowest densities of wolverines occur in the ecoprovinces that have the lowest habitat diversity and prey abundance-the Boreal Shield and the Boreal Plains ecodivisions. These ecodivisions are among the first where wolverine disappeared with the advance of civilization.

Stand level

Preferences for some forest cover types, aspects, slopes, or elevations have been primarily attributed to a greater abundance of food (Gardner 1985; Banci 1987), but also to avoidance of high temperatures and of humans (Hornocker and Hash 1981). The greater use of subalpine coniferous habitats by males in southwest Yukon in winter was speculated to be due to higher densities of ungulate kills in these habitats (Banci 1987). Similarly, the use of alpine areas in south-central Alaska in summer was attributed to the arctic ground squirrels there (Whitman et al. 1986). In Montana, Hornocker and Hash (1981) believed that wolverines used higher ranges during the snow-free season because they were avoiding high temperatures and human recreational activity (Hornocker and Hash 1981).

Predation may influence wolverine habitat use, depending on the predator complement in the envi-

ronment, including humans. In south-central Alaska, wolverine use of rock outcrops was greater than the availability of those areas during summer (Gardner 1985), perhaps because rock outcrops were being used as escape cover from aircraft. However, wolverines may have also been hunting marmots and collared pikas (*Ochotona collaris*) (Gardner 1985). Wolverines may climb trees to escape wolves (Boles 1977, Grinnell 1921), although if the trees are not high enough, such attempts may be unsuccessful (Burkholder 1962). Wolverines are found in a variety of habitats and do not appear to shun open areas where wolves are present. Wolverines occur locally with cougars, especially in British Columbia and the northwestern United States. Trees would not be an effective defense because cougars are adept at climbing. It is likely that wolverines use various habitat components, such as rock outcrops or trees, for escape when they feel threatened.

Aside from anecdotal reports, only Hornocker and Hash (1981) have reported on the use of resting sites by wolverines in forested habitats. Overhead cover may be important for resting sites as well as natal and maternal dens. Resting sites in Montana were often in snow in timber types that afforded cover (Hornocker and Hash 1981).

Impacts of Land-Use Activities

The impacts of land-use activities on wolverine habitat are likely similar to those that have been described for grizzly bears, another species that has been negatively impacted by land-use activities. Agriculture, domestic cattle ranges and grazing, forestry, mineral and petroleum exploration and development, hydroelectric power development, human settlement, population growth, and recreation all have affected the productivity and integrity of habitat within wolverine range (Banci et al., in press). Habitat alterations have been limited in northern ecoprovinces but have been extensive in the northwest United States, southern British Columbia and Alberta.

The greatest impacts on the potential of the land to support wolverines in Canada have occurred in the Boreal Plains ecodivision because of extensive agricultural development; in the Pacific Northwest Coast and Mountains because of forestry, settlement, and access; in the Central British Columbia Plateaus because of losses of productive riparian areas and wetlands, and predator removal because of conflicts with agriculture; and in the Shining Mountains because of water impoundments and highway construction (Banci et al., in press). Impacts of habitat loss and fragmentation have been large in all ecoprovinces in the northwestern United States, except for those areas in parks or other refugia.

The impacts of logging and associated activities on wolverines and wolverine habitat can only be surmised. A preference by wolverines for mature to intermediate forest in Montana (Hornocker and Hash 1981) was not apparent in southwest Yukon (Banci 1987) or in south-central Alaska (Gardner 1985). Hornocker and Hash (1981) reported that although wolverines in Montana occasionally crossed clearcuts, they usually crossed in straight lines and at a running gait, as compared to more leisurely and meandering patterns in forested areas. The study area in Montana was the only one a portion of which had been logged (Hornocker and Hash 1981). However, no differences in movements, habitat use, or behavior was noted between wolverines occupying the half of the area that was logged and the half that had not (Hornocker and Hash 1981).

Wolverine populations that have been or are now on the edge of extirpation have been relegated to the last available habitat that has not been developed, extensively modified, or accessed by humans (such as roads and trails). On Vancouver Island, wolverines survive mainly in habitats that are largely inaccessible, the central mountain ranges and the west coast, in contrast to an historical distribution that ranged from coast to coast. They have largely been maintained in western Alberta by the extensive system of national parks. In Montana, the persistence of wolverine despite years of unlimited hunting and trapping has been attributed to the presence of large, isolated wilderness refugia: Glacier National Park and the Bob Marshall Wilderness (Hornocker and Hash 1981). In Washington and Oregon, wolverine reports come from the largely protected North Cascades. Similarly in Idaho, Wyoming, and Colorado, wolverines generally are sighted in remote and mountainous areas. The perception that wolverines are a high-elevation species has arisen because where wolverine are surrounded by people, they are usually found in the most inaccessible habitats, the mountain ranges.

Some wolverines tolerate civilization to the extent of scavenging at dumps in northern communities and living adjacent to urban areas in the north (LeResche and Hinman 1973; Holbrow 1976). They use food and garbage at trapper cabins and mines and have fol-

lowed traplines, systematically removing furbearers from traps. This is opportunistic foraging behavior, inasmuch as there is no evidence that human food sources are used extensively or that wolverines become habituated to human food, except for those that are starving. The presence of humans may conflict directly with wolverines. Hornocker and Hash (1981) suggested that human access on snowmobiles or all-terrain vehicles in winter and early spring could cause behavioral disturbances.

Wolverines seem to have been most affected by activities that fragment and supplant habitat, such as human settlement, extensive logging, oil and gas development, mining, recreational developments, and the accompanying access. Despite their association with remote and generally wild habitats, information is insufficient to define what wilderness components wolverines require or to gauge when the impacts of a land-use activity have been excessive.

Management Considerations

1. With our current dearth of knowlege, conserving wolverine populations may require large refugia, representative of the vegetation zones that wolverine occupy and connected by adequate travel corridors. Refugia have a dual purpose, also serving as a source of dispersing wolverine for other areas. Appropriate refuge sizes are unknown but will depend on habitat suitability. The lower the wolverine density, the larger the refuge necessary. It is best to think of refuge size in terms of wolverine reproductive units, 1 male and 2-6 females. How many reproductive units in a refuge are necessary to ensure population maintenance and dispersal? If population characteristics such as density and recruitment are known, modeling can help to answer this question.

2. The dispersal and travel corridors that connect refugia, at least for males, likely need not have the habitat attributes necessary to support self-sustaining populations. Atypical or low quality habitats may be important to wolverines if they connect otherwise isolated populations and allow for genetic exchange or colonization. Because females establish home ranges next to their natal area and their dispersal distances are less than for males, requirements for dispersal corridors may be more specialized. The biggest limiting factor in recolonization likely is the dispersal of young females.

3. Because refugia for wolverines will no doubt be very large, the species will benefit by being part of a large carnivore conservation strategy in which connected refugia are established for grizzly bears, wolves, cougars, and wolverines. Such a strategy will help to ensure that the entire range of wolverine habitat needs will be accommodated and lessens the chance that refugia will not be large enough or that an important requirement will not be adequately met.

4. Until more information becomes available, habitat management prescriptions that successfully provide for the life needs of species such as the American marten, fisher, and lynx and their prey will also provide for the needs of wolverine at the stand level. However, it is not known whether this will provide for wolverine habitat needs at the landscape or larger scales.

Research Needs

1. Study the habitat needs of wolverine in forests, because there is no sound basis for developing habitat management prescriptions at the stand level. Information that will allow development of recommendations for road densities, sizes of areas on which timber is cut, minimum cover requirements, natal dens, resting sites, and coarse woody debris is required.

2. Remote censusing devices such as cameras may be useful to determine the use of habitats by wolverine and to address the impacts of forest harvesting.

3. To determine appropriate refuge locations and sizes and travel corridors for wolverines, their current distribution at both small and large map scales, with current and projected land-use activities, must be mapped. This process will also assist in identifying habitats that have been fragmented and isolated and populations that are isolated. In line with the recommendation to consider the wolverine as part of a large carnivore conservation strategy, much of this work in the conterminous United States can be coordinated with that occurring for grizzly bear ecosystems.

4. If the dispersal of young females is the primary limiting factor in the recolonization of denuded habitats, providing for their dispersal needs will be important in recovery efforts. Information on the movements of dispersing females and their use of habitats is necessary to ascertain the appropriate composition and location of travel corridors.

5. Consideration of wolverine habitat needs in managed forests is complex because wolverines use habitats at different scales. Research is needed on what it means for wolverine to use habitats at the landscape scale and how this can be translated into habitat management guidelines. Attributes that may

be important at the landscape scale are the percentage of different seral stages; shape, placement and numbers of timber cuts; the time between cuts; and locations of travel corridors. Criteria for recreational developments such as ski areas, hiking trails, and snowmobile and all-terrain vehicle use also need to be developed at the landscape scale.

HOME RANGE

Home ranges of adult wolverine in North America range from less than 100 km^2 to over 900 km^2 (table 6). The variation in home range sizes among studies partly may be related to differences in the abundance and distribution of food. Wolverines in the southwest Yukon and in southcentral Alaska concentrated their use at large ungulate carcasses (Gardner 1985; Banci 1987) and locations of spawned salmon (Banci 1987). Localized areas of high food availability were cited as the reason for small home ranges in southwest Yukon (Banci and Harestad 1990). In northwest Alaska, food levels were particularly low and dispersed because of the absence of overwintering caribou and home ranges of wolverine were larger than all others reported (Magoun 1985).

The presence of young restricts movements and home range size of females (table 6). Yearly home ranges for a female with young was 47 km^2 (discounting 2 long-distance movements) in southwest Yukon (Banci and Harestad 1990); 100 km^2 each for 2 females in Montana (Hornocker and Hash 1981); a mean of 105 km^2 in south-central Alaska (Whitman et al. 1986); and a mean of 70 km^2 in northwest Alaska (Magoun 1985). Male home ranges are typically larger than those of females (table 6). Spring and summer home ranges of adult males, but not adult females, increased during the breeding season in Alaska and Montana (Hornocker and Hash 1981; Gardner 1985; Magoun 1985) but not in the Yukon (Banci and Harestad 1990). In the latter, localized and abundant food may have been responsible for females being readily available to the adult male, making extensive breeding movements unnecessary (Banci and Harestad 1990).

This pattern of home range use is consistent with a carnivore spatial strategy in which the spacing of females underlies the distribution of males, at least

Table 6.--Annual home ranges (km^2) of wolverine in North America.

Location	Mean	Range	*n*	Reference
Adult males				
Northwest Alaska	666	488-917	4	Magoun 1985
Southcentral Alaska	637		1	Gardner 1985
Southcentral Alaska	535		4	Whitman et al. 1986[1]
Southwest Yukon	238		1	Banci 1987
Montana	422		9	Hornocker and Hash 1981
Subadult males				
Southwest Yukon	526		1	Banci 1987
Idaho	435		1	Copeland 1993[2]
Adult females with young				
Southwest Yukon	139[3]		1	Banci 1987
Southcentral Alaska	105[4]		3	Whitman et al. 1986
Northwest Alaska	73	55-99	3	Magoun 1985
Montana	100		2	Hornocker and Hash 1991
Adult females without young				
Northwest Alaska	126	56-232	6	Magoun 1985
Southwest Yukon	272	202-343[5]	2	Banci 1987
Montana	388	963 (max.)	11	Hornocker and Hash 1981
Idaho	338	160-516[6]	2	Copeland 1993

[1] *Estimated using the relationship between time of monitoring and home range size.*
[2] *90% minimum polygon home range is 369 km^2.*
[3] *If two long-distance movements are excluded, home range is 47 km^2.*
[4] *Estimated using the relationship between time of monitoring and home range size.*
[5] *If I long-distance movement is excluded for each female, home ranges are 153 and 157 km^2, with a mean of 155 km^2.*
[6] *90% minimum polygon home ranges are 82 and 447 km^2; core harmonic mean ranges are 79 and 306 km^2.*

in the breeding season, but food underlies the distribution of females (Sandell 1989). Home ranges of females should reflect the minimum size necessary to obtain food more than those of males (Sandell 1989). Consistent with this prediction, wolverine females typically cover their home ranges uniformly, unless they have kits and concentrate their movements at natal dens or rendezvous sites (Gardner 1985; Hornocker and Hash 1981). Males, instead, typically have one or more foci of activity within the home range (Hornocker and Hash 1981; Gardner 1985).

Winter home ranges typically overlap with those used in the snow-free season but also include different habitats, even if there are no significant differences in the size of seasonal home ranges (Hornocker and Hash 1981; Magoun 1985; Banci 1987). Differences between seasonal home ranges can be attributed to changes in prey distribution and availability. Wolverines of both sexes appear to maintain their home ranges within the same area between years (Magoun 1985; Banci 1987). There may be slight changes in the yearly boundaries of home ranges with the addition of juvenile females adjacent to the natal area, with mortality, and with immigration. For example, when a resident dies, a neighbor may assume part of the vacant home range (Magoun 1985; Banci 1987).

Home ranges of subadults, especially males (table 6), are transitory areas used before dispersal. Typically, home range use by immature males is characterized by extensive movements out of the natal home range (Gardner 1985; Magoun 1985; Banci 1987). Adults may make temporary long-distance movements outside the usual home range, which are apparently not related to dispersal. Adult females in Yukon made one or two long-distance movements in summer only, inflating the size of their annual home ranges if these movements were included (table 6). Such excursions were also observed frequently for both sexes in Montana (Hornocker and Hash 1981) and were documented for females in northwest Alaska (Magoun 1985).

Spatial Patterns

The basic spatial pattern in Mustelidae has been described as intrasexual territoriality, in which only home ranges of opposite sexes overlap (Powell 1979). In general, spatial patterns in wolverines are consistent with this, although partial overlap of home ranges of some wolverines of the same sex is common. In northwest Alaska, home ranges of adult males were exclusive in winter, whereas those of adult females overlapped only in winter (Magoun 1985). In southwest Yukon, spatial but not temporal overlap of adult female home ranges occurred during winter (Band and Harestad 1990). It is likely that neighboring adult females are related, resulting in a greater tolerance for overlap between individuals (Magoun 1985). Home ranges of adult males and females overlap extensively, with the range of one male covering the ranges of 2 to 6 females (Magoun 1985; Banci 1987). Also, adult home ranges overlap with those of immatures (unpublished data in Whitman and Ballard 1983; Magoun 1985; Banci and Harestad 1990). Preliminary data for Idaho is consistent with this pattern, with overlap occurring only between juveniles and adults and between sexes (unpublished data in Copeland 1993).

In northwest Montana, Hornocker and Hash (1981) attributed the extensive overlap of wolverine home ranges of both sexes and all ages to the effects of human predation, which removed individuals before they established tenure, contributing to behavioral instability. This study was conducted from 1972 to 1977 and until 1975, the wolverine in Montana was classified as a predator and unlimited killing was permitted (Hornocker and Hash 1981). It was not until the last 3 years of their study that trapping was prohibited in their study area. Considering that Montana had only recently been recolonized by wolverine, it is possible that the individuals that were studied were not able to establish home ranges. Hornocker and Hash (1981) could not ascertain whether individuals were transients or residents. It would be interesting to know if now, almost 20 years after protection, adult wolverine have established intrasexual territories.

At abundant and concentrated sources of food, such as large carrion or accumulations of spawned salmon, tolerance among adult wolverines appears to increase and adult individuals of the same sex may feed concurrently at the same site, or at the same food source (Banci 1987). It is unlikely that the dominance structure normally present in areas that do not have such foods breaks down. Rather, the individual home range boundaries of wolverines should shrink if it is not possible or profitable for them to defend an abundant food source, consistent with Lockie's (1966) prediction that individual home ranges will vary in exclusiveness depending on the concentration of resources in different seasons or habitats.

Communication

Wolverines have complex structures that may be important for chemical communication, including anal glands, a possible abdominal gland (Hall 1926), and plantar glands on the rear feet (Buskirk et al. 1986). The morphology of these structures has not been well studied. Wolverines also mark by urinating, defecating, scratching the ground, and biting trees (Koehler et al. 1980; Magoun 1985). Defecation does not appear to be an active form of scent marking although urination on older scats sometimes occurs, with these scats then acting as scent posts (Magoun 1985).

Urination appears to be the primary means of communication, often occurring at raised and traditional landmarks (Koehler et al. 1980; Magoun 1985). After urination, abdominal rubbing was the second-most used method of communication in captive wolverines (unpublished data in Long 1987). Marking with the anal glands appears to be primarily used as a fear or defense mechanism (Seton 1929; Krott 1960; Magoun 1985). Koehler et al. (1980) reported some of the few data on the use of musk in scent marking.

Wolverine devote considerable energy to scent marking, deviating from their line of travel specifically to mark objects (Koehler et al. 1980; Magoun 1985). As in other carnivore populations, scent marking in wolverines likely serves as a means of monitoring the reproductive status of individuals, assists in foraging, and maintains separation of individuals in space and in time (Gorman and Trowbridge 1989).

Management Considerations

1. Even within an ecoprovince, home range size and use by wolverine differ because of differences in habitats, in the distribution and availability of food, and in the intensity and extent of habitat alteration and other human influences. Home range sizes have been used to estimate densities in areas other than where they were determined, based on the assumption of intrasexual home range exclusivity. Because of the few data available, wolverine densities determined using home range size cannot be reliably extrapolated to the rest of an ecoprovince or used to compare ecoprovinces.

2. Localized and seasonally abundant sources of food such as carrion, salmon-spawning streams, and possibly berry patches are important to wolverines and receive heavy use within the home range. Land use activities may impact such habitats.

3. At the landscape level, the wolverine's large home ranges need to be considered in forest management planning. The area required by a wolverine reproductive unit, a male and 2-6 females, may be an important consideration in landscape planning.

Research Needs

1. Home range size and use that have been determined in or adjacent to remote undeveloped areas are biased to northern habitats and generally are not known for western forests. Opportunity is quickly eroding to determine wolverine home range and habitat use in western North American forests where habitats have not been modified and populations have not been heavily exploited. However, without such comparative information, the impacts of land-use practices such as forestry, intensive silviculture, and oil and gas exploration and development on wolverine home ranges and habitat cannot be assessed.

2. Scent marking is an important mechanism for communication. Field studies need to continue to examine the role of scent marking in population maintenance, both in established populations, and by transients and dispersers. This information can help in understanding how vacant habitats are colonized and how exclusive home ranges are established. Changes in marking behavior may also be the first evidence of the impacts of land-use practices, human activity, and habitat alterations on wolverine.

MOVEMENTS AND ACTIVITY

Wolverines can travel long distances in their daily hunting, 30-40 km being "normal" (Krott 1960; Haglund 1966; Pulliainen 1968). These distances, determined by snow-tracking, provide better estimates of the actual distances covered than does telemetry. In northwest Alaska, actual movements were 33% greater than straight line distances between telemetry locations (Magoun 1985).

Adult males generally cover greater distances than do adult females (Hornocker and Hash 1981; Gardner 1985; Magoun 1985) and may make longer and more direct movements (Hornocker and Hash 1981). During late winter, lactating females with young move less than solitary adult females (Gardner 1985; Magoun 1985). In May and June, hunting mothers periodically return to their young that have been left at rendezvous sites (Magoun 1985). In northwest Alaska, females returned to rendezvous sites at least

daily (Magoun 1985). Kits were moved to new rendezvous sites every 1-9 days and more frequently as they grew older (Magoun 1985). By June, kits were moved every 1-2 days (Magoun 1985). When her kits were 4-11 weeks old, a female in central Idaho used 18-20 den sites, moving her kits a total of about 26 km (unpublished data in Copeland 1993).

In the southwest Yukon, all 3 resident adult females made 1 or 2 long-distance movements of 11-31 km from their home range boundaries that lasted 1-2 weeks in summer (Banci 1987). In northwest Montana, wolverines of both sexes made frequent long movements out of their home ranges that lasted from a few to 30 days, and they always returned to the same area (Hornocker and Hash 1981). These long-distance movements appear to be temporary and not attempts to expand the home range. Whether these movements are exploratory or whether wolverine are returning to previously known feeding locations is unknown.

Except for females providing for kits or males seeking mates, movements of wolverine are generally motivated by food. Wolverines restrict their movements to feed on carrion or other high quality and abundant food sources (Gardner 1985; Banci 1987). In south-central Alaska, wolverines fed on ground squirrels in alpine areas in the spring and summer (Gardner 1985). In winter, they moved to lower elevations to feed primarily on wolf-killed and winter-killed moose and caribou (Whitman et al. 1986).

Dispersal

Young females typically establish residency next to or within the natal home range (Magoun 1985). Although some immature females disperse, males are more likely to do so. Male wolverines may disperse either as young-of-the-year or as subadults (Gardner 1985; Magoun 1985; Banci 1987). Dispersal can include extensive exploratory movements (Magoun 1985; Banci 1987). A subadult male left his home range of at least 7 months, stayed away for 2 months and then returned, remaining only 2 weeks (Banci 1987).

Magoun (1985) hypothesized that dispersal of young occurred as early as January and as late as May. The increased movements of young-of-the-year males, either exploratory or dispersal, make them susceptible to trapping as early as November (Banci 1987). The longest documented movement was 378 km by a male from southcentral Alaska to the Yukon over eight months (Gardner et al. 1986). Adult males appear to influence the dispersal and settlement of immature males (Banci 1987; Gardner 1985).

Rivers, lakes, mountain ranges, or other topographical features do not seem to block movements of wolverines (Banci 1987; Hornocker and Hash 1981). At times, wolverines will use rivers and streams as travel routes probably because prey species also use these travel routes (pers. obs.). Considering the wolverine's avoidance of human developments, extensive human settlement and major access routes may function as barriers to dispersal.

Management Considerations

1. In some areas, wolverines in alpine and subalpine habitats may be subjected to intense recreational activity in the spring and summer. This disturbance may impair kit survival if females are forced to use less secure den sites. Recreational activity may be a concern if den sites are limiting because wolverine have been relegated to high elevation areas due to extensive habitat loss and alteration. Access management plans may need to consider all-terrain vehicles, aircraft, and travel on foot and travel on horseback to protect denning females.

2. The long movements of wolverines suggest that recolonization of vacant habitats is not a concern. However, because of the tendency of young females to settle next to the natal area, recolonization may be delayed unless the source population has a high kit survival and young females are forced to disperse to find vacant habitats in which to establish home ranges. If dispersal is to be relied upon as a means of reestablishing populations, the productivity of the source population is important. Dispersal corridors that supply the requirements for young females are also important.

Research Needs

1. Dispersal distances of female wolverine may be considerably less than those of males. To predict the potential for success and length of time necessary for recolonization of vacant habitats, information is needed on the survival rate and distances dispersed by young females.

2. The long-distance movements made by adult resident wolverines appear to be rare enough that they have little impact on habitat or home range use. However, it is unlikely that a species would make such movements unless they conferred a positive benefit on survival. Future studies should attempt to document the nature of these movements, their occur-

rence over time, whether both sexes are involved, and whether factors outside the home range such as habitat, food availability, or other wolverine are influences.

COMMUNITY INTERACTIONS

Primarily scavengers, wolverine clean up after the more efficient hunter carnivores. They prey on species smaller than themselves, if abundant. Even where habitats are optimal, wolverines occur at such low densities that it is unlikely they have a major effect on numbers of any other species. They are not important food for any other species. As scavengers, they not only depend on carnivores like wolves, cougars, and bears, but conflict with them, occasionally being killed by them. Their most important predator is humans, through trapping and hunting. Likewise humans indirectly affect wolverines through prey, impacts on other carnivores, and habitat changes.

Wolverine and Prey

The presence of large mammals underlies the distribution and abundance of wolverines, especially in northern environments. North of treeline, the distribution of wolverines appears to be tied to that of the barren-ground caribou. Wolverines can survive for short periods if caribou are absent but may not reproduce during these times (Magoun 1985). Wolverine are too large to subsist solely on small prey. Nothing is known about the population dynamics of wolverines that have access to highly nutritional food sources, such as salmon in coastal and interior areas, intertidal habitats, and marine mammal carcasses. It is possible that locally productive wolverine populations have been lost in North America because of hydroelectric development and the subsequent loss of major salmon runs.

In the boreal ecoprovinces of western Canada and Alaska, the primary large mammal species for wolverine are caribou and moose. South of treeline, large mammal carrion is provided primarily by cervids, likely because their availability is greater than that of bovid species such as mountain goat and mountain sheep. In the Shining Mountains, Northern Rocky Mountain Forest, Pacific Northwest Coast and Mountains, and Sierra Nevada ecoprovinces, deer and elk are important. Although large carrion is a key element in the wolverine diet, the diet requires scavenging and hunting smaller prey. A prey base diverse in size and in species is important because large carrion is not always available. Snowshoe hares, especially, are important in diets from northern ecoprovinces. An abundance of large mammal carrion or a diverse prey base does not guarantee the presence of wolverines, especially if other life needs, such as denning habitat or travel corridors, are not met.

Wolverines, Wolves, and Humans

In their foraging activities, wolverine occasionally conflict with and may be killed by wolves, cougars, and bears. Predators are not likely to be a significant mortality factor on adult wolverines because they are killed only opportunistically, although predation on kits may occur.

Although few records were kept, wolverines likely were heavily impacted by the extensive wolf eradication programs carried out over much of North America early in this century. Private control efforts began shortly after the arrival of Europeans in the early 1600's (Stardom 1983) and government agencies took over in the 1950's and 1960's (Carbyn 1983). In Manitoba and the Northwest Territories, 1 wolverine was killed for each 8 to 9 wolves (van Zyll de Jong 1975; Kelsall 1968); an average of 1,800 wolves were killed yearly (Heard 1983). Trappers in the early 1900's also regarded wolverine as vermin because of their propensity to raid traplines and cabins, so trappers used strychnine as a means of trapping (Gunson 1983; Smith 1983).

The shrinking range of wolverines coincided with that of wolves in the late 1800's and the early 1900's. In some areas, predator control was coupled with the decimation of large mammal populations, such as the northern caribou herds (Heard 1983; Luttich 1983), reducing food available to wolverines. After the termination of widespread control in much of Canada, wolves recovered quickly but wolverines did not. This lack of recovery was most evident in eastern North America.

Wolverines and Wilderness

Wolverines appear not to tolerate land-use activities that permanently alter habitats, such as agriculture, and urban and industrial development. Unlike species such as coyotes (*Canis latrans*), black bears, raccoons (*Procyon lotor*), wolves, and some ungulate species in agricultural areas, wolverines generally do not eat the human foods that accompany human habitation. More than the actual loss of habitat or the

presence of humans, it is possible that the habitat fragmentation and access that result from land-use activities have the greatest impacts on wolverine.

CONSERVATION STATUS

A main theme that has emerged is that the information necessary for the management and conservation of wolverine populations in western forests is not available. Of paramount need is basic information on the occurrence and distribution of wolverines in the conterminous United States, and on whether these populations are self-sufficient or dependent on dispersers from Canada. With increaseing development and access in southwestern Canada and the northwestern United States, some populations may have already become isolated.

Until research can delineate the extent and nature of genetic variability among populations---and until research can determine whether wolverine ecotypes occur-then the conservative approach is to ensure that the range of variability is not degraded, either through loss of populations or continued population reductions. Although little information is available for mammals, higher genetic diversity at southern latitudes may characterize not only species but populations within species and genes within populations (Ledig 1993).

Because of the wolverine's large home range and extensive movements, it may appear that specific habitat attributes are not important and recolonization of vacant habitats is not a concern. However, natal and maternal dens may require a high degree of structural diversity and may be limiting in habitats that have been extensively modified by logging or other land-use practices. Insufficient denning habitat may serve to decrease the already low reproductive potential of wolverine. The dispersal of young females is likely the limiting factor in the recovery of vacant habitats. Successful recolonization may depend on sufficient recruitment from the source population and adequate dispersal corridors. Corridors that meet the needs of dispersing males may not do so for young females.

The key to maintaining wolverine populations is the establishment of large protected areas representative of the ecoregions that wolverine occupy and connected by adequate travel corridors. Refugia are important for providing dispersers to surrounding habitats, but it is unlikely that they will guarantee population persistence. Wolverine habitat needs must be accommodated at more than one scale: at the stand scale to meet requirements for food and dens, and at the landscape scale to meet requirements for home range sizes, travel corridors, and dispersal corridors.

The Future of Wolverine Populations

Wolverines in the western conterminous United States exist in small populations largely in inaccessible areas. Populations in northwest Montana have the greatest likelihood of long-term persistence because they are contiguous with protected areas in British Columbia and Alberta. The persistence of populations in Idaho, Oregon and northwest Wyoming are less certain but can be enhanced if connected large refugia are established within the Shining Mountains and the Northern Rocky Mountain Forest ecoprovinces. The Colorado population, if it still exists, may be isolated by the Wyoming and Central Rocky Mountain Basins. A recovery evaluation should consider whether the Colorado Rocky Mountains ecoprovince historically supported self-sustaining wolverine populations.

The future of wolverine populations in the Pacific Northwest Coast and Mountains ecoprovince is uncertain because of human settlement and dispersal barriers and possible isolation. Wolverines in the Sierra Nevada ecoprovince may already be isolated. Isolated populations maintained by refugia most certainly will survive in the short term. However, without dispersal corridors, their long-term persistence is in doubt.

With the current level of land-use activity, it may not be possible to provide sufficiently large refugia for wolverines where populations are not contiguous with habitat from British Columbia and Alberta. Even large national parks such as Yellowstone are considered too small to maintain self-sustaining populations of certain bears and other upper level carnivores (Soule 1980; Salwasser et al. 1987). An evaluation of whether there is sufficient habitat to support self-sustaining populations and to provide for dispersal corridors in the Pacific Northwest Coast and Mountains, Sierra Nevada, and Northern Rocky Mountain Forest ecoprovinces is required. Such evaluations will likely show that the long-term persistence of these populations is dependent on recovery efforts.

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Chapter 6

The Scientific Basis for Conserving Forest Carnivores: Considerations for Management

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INTRODUCTION

The reviews presented in previous chapters reveal substantial gaps in our knowledge about marten, fisher, lynx, and wolverine. These gaps severely constrain our ability to design reliable conservation strategies. This problem will be explored in depth in Chapter 7. In this chapter, our objective is to discuss management considerations resulting from what we currently know (and don't know) about these four forest carnivores.

The authors of each species chapter have summarized the current state of knowledge about the biology and ecology of each species. Management considerations might lead to modifications or restrictions in the way these species or other resources are managed, given that the conservation of one or more forest carnivores is a management objective. As appropriate, we will compare and contrast management considerations for all four species and identify management considerations that apply to the population status or habitat quality for two or more species at the same time.

These discussions should not be interpreted as management recommendations. Rather, we intend to broadly address management activities likely to influence the persistence of forest carnivore populations. The information we have drawn upon is limited and often derived from studies conducted over brief time periods with insufficient replication and small sample sizes (see Chapter 1 for further discussion of these limitations).

All of the forest carnivores are trapped for their fur within some portion of their geographic range. Because of their status as furbearers, these species require population management involving the regulation of trapping seasons and harvest levels. We will not ignore the need for management of this significant source of mortality, but our primary focus in this chapter will be on the management of habitat. Clearly, habitat management cannot be expected to maintain or increase population levels where trapping pressure is not carefully regulated. It is our hope that an increased awareness among all managers about the conservation status and habitat needs of these carnivores will foster improved cooperation. Federal agencies are responsible for managing much of the habitat occupied by these furbearers. State and provincial agencies are responsible for regulating trapping. These responsibilities cannot be isolated by these agencies if successful conservation strategies are to be developed.

Spatial Relationships

The forest carnivores under consideration here range over extremely large geographic areas. They occupy home ranges that vary in size from under 16 km^2 for marten to over 900 km^2 for wolverine. Management and conservation of these species can only be understood over a range of spatial scales. In this chapter, we consider four spatial scales nested in a hierarchy of increasing size. These scales are ecologically linked and generically equivalent to scales used in Ecomap (Bailey et al. 1993) and ecoprovinces (Demarchi, Appendix A). Our primary interest is in habitat needs of each carnivore species considered at the stand, landscape, ecoprovince, and region levels defined as follows:

Stand is a homogeneous habitat patch such as a cutting unit or a relatively small-scale burn or blowdown in any stage of regrowth. Resting and denning requirements can usually be described as structural characteristics of individual stands or even unique structures within stands. Habitats selected for foraging may include certain stand structures but require several adjacent stands. Stands are always smaller than the average home range size for each species.

Landscape, in our hierarchy of geographic scales, is defined as an aggregation of stands. Landscapes are not precisely defined in terms of the geographic area they may encompass but, in order to be meaningful for animals, they must be defined in relation to the ecology and mobility of each species under consideration. Thus, landscapes may vary in the following discussion as a function of the species under discussion, but they will always be large enough to encompass one or more average home ranges (see Chapter 7 for further discussion).

Ecoprovince recognizes an even larger spatial scale encompassing an aggregation of landscapes as defined above. Ecoprovinces are areas where the climate and landforms provide a common influence on vegetation, on the behavior and dynamics of animal populations, and on some land-use activities. Management considerations at this scale involve population viability over areas so large they encompass more than one agency's jurisdiction. Management strategies may require at least multi-jurisdictional cooperation.

Region. At the greatest spatial scale considered here, ecoprovinces are aggregated into geographic regions, which include such areas as the Rocky Mountains or the Sierra Nevada. Species persistence must be considered at this scale. Management strategies may require international cooperation.

Categories of Management Considerations

We will consider three broad categories of management considerations for forest carnivores: habitat, populations, and species. The first section discusses considerations for management through the management of habitats beginning at the stand level and progressing through landscapes and ecoprovinces. The latter sections represent management considerations of a very broad nature, relating to either populations and metapopulations within an ecoprovince portion of the species' range or for the entire species in a geographic region or even the North American continent.

HABITAT MANAGEMENT CONSIDERATIONS

In the following synthesis of habitat management considerations, we first examine habitat components within stands to emphasize the hierarchical nature of these spatial scales and the fact that adequate habitat for any of these forest carnivores can only be maintained by providing suitable habitat components at all spatial scales.

Stands and Components Within Stands

Stand-level habitat for marten is described as late-seral mesic conifer stands with complex structure near the forest floor. Habitats occupied most commonly by fishers have an overhead canopy and complex physical structure, including dead and down material as well as low branches or shrubby vegetation near the forest floor. Lynx appear to be somewhat more tolerant of openings, but they also prefer forest habitats with overhead cover and vegetation near the ground. For these three species, physical structure of the forest appears to be more important than species composition of the vegetation, and while suitable habitat is not necessarily old growth, there is little question that some preferred components are representative of old-growth structures. While only suggestive, we interpret this as an indication that late-successional forest stands or their structural features are essential stand-level components of habitats for marten, fisher, lynx, and probably wolverine.

Wolverines, however, seem less sensitive to overhead canopy cover or vegetation near the ground, possibly because they are often detected in alpine or subalpine situations. When detected at lower elevations, they show a preference for mature to intermediate aged forests. The essential component of wolverine habitat may be isolation and the total absence of disturbance by humans. Where isolation happens to coincide with forests, as it often does in designated wilderness areas of the United States, wolverines will be found in forest habitats.

Specific within-stand structures for denning, resting, and foraging are somewhat different for each of these carnivores, but all include late-seral stand structures. Fisher and marten are more selective of habitat for resting than of habitat for foraging and appear more selective for natal den sites than for resting sites. Within stands, these considerations are thought to apply equally to all four species. Thus, the denning site is considered to be the most unique and possibly limiting of within-stand habitat structures.

Denning Sites

With the exception of the marten, the number of dens reported in the literature is too small to provide meaningful structural descriptions of den characteristics for any of these small forest carnivores. Only two natal dens of fisher, and four of lynx, have been described in the western mountains, and wolverine den information, mostly from Europe, is biased toward tundra. This lack of specific description is compounded by the fact that natal den sites (i.e., parturition sites) of all four species are usually abandoned as soon as the young can be moved to a maternal or rearing den. Such movement of young may take place several times prior to their independence.

Stands in which dens of marten, fisher, lynx, and (to a lesser extent) wolverine have been found are characterized by downfall, snags, large trees, hollow trees, and stumps. Similar characteristics describe wolverine denning areas in forest habitats. These are very specific habitat settings that provide structural diversity and cover for the young. We do not know which components may limit reproductive success; although the marten literature indicates a preference for denning in logs, large trees, and snags. For marten, fisher, and lynx, at least until definitive habitat descriptions become available, managers can probably provide denning habitat by preserving and recruiting large snags, decadent broken-top trees, and downfall as potential components of structural diversity necessary for den sites in closed-canopy forest.

Unlike the three smaller carnivores, wolverines may not require snags and large trees for natal den sites. Wolverine natal dens have been found in snow tunnels, hollow trees, or even caves in the ground. In forested habitats, however, the structural diversity provided by large snags, fallen logs, and stumps will likely provide natal den sites for wolverines. Isolation from human disturbance also appears to be an important den-site requirement for wolverines. Once the young can be moved, maternal dens of marten, fisher, and lynx, and rendezvous sites of wolverine, are also located in habitats characterized by structural diversity.

Resting Sites

Marten and fisher rest primarily in large downed logs and snags, but live trees are also used. Downfall is essential for marten in winter since virtually all rest sites are subnivean and downed material that protrudes through the snow provides access. Fisher resting sites are selected for warmth in winter and to prevent overheating in summer. Fisher and wolverine dig snow tunnels; brushpiles, logs, stumps, and hollow trees have also been used. Marten also rest in rock piles, squirrel middens, large-diameter trees, and witches' brooms. Resting sites for all four species again demonstrate the need for structural diversity within stands.

Foraging Areas

Foraging areas are habitats where important prey species are available to each carnivore. The similarities and some major differences among the foraging habitats selected by forest carnivores are a reflection of the foraging behavior of the predator and the habitat requirements of the primary prey. Marten capture a wide variety of small mammals, but the primary food source appears to be ground-dwelling voles found in forests with complex structure near the ground. Downed dead material is particularly important in providing access to subnivean space during the winter. The lynx, on the other hand, is considered dependent on snowshoe hares over much of its range; and the early successional forests that provide cover and browse for hares are the habitats favored by lynx for hunting. Hares are also important components in the diets of fisher and wolverine, but the fisher appears far less tolerant of open, early successional habitats favored by the snowshoe hare. Fishers are a specialized predator of porcupines,

a prey species for which they have almost no competition, but fishers will eat any small- to medium-sized mammal or bird they can capture. They also readily eat carrion but are not nearly as dependent on this resource as the wolverine, for which the carrion of large ungulates is a primary food source.

In describing habitat structures required for hunting, a common behavioral thread for all of these carnivores is some degree of reluctance to forage in the open. Openings, either natural or created by human actions, are not well tolerated and a common behavior pattern for fisher and lynx in openings is a quick crossing unless the vegetation supports high numbers of a desired prey species. Wolverine have also exhibited this behavior in forested habitats, and marten tend to avoid use of openings. Fishers will hunt in open-forest situations, but they minimize travel in the open. In diverse landscapes, lynx will use habitats with overhead cover to move between foraging and denning areas. Clearcuts, specifically, are avoided until canopy closure is reached or understory herbaceous growth has become particularly attractive to snowshoe hares. Even under these conditions, lynx require cover for security and for stalking prey.

Wolverines will almost certainly hunt in the same kinds of habitats used by other forest carnivores, but there is no evidence hunting by wolverines is limited by habitat structure. Primarily a scavenger, rather than a hunter, the wolverine forages where carrion can be found.

Stand Management to Favor Prey

More than the other forest carnivores, reproductive success of lynx has been shown to be highly correlated with the density of snowshoe hare populations. In northern boreal forests, increases in hare numbers are followed by increases in lynx, and conversely, a decline in hare abundance will affect reproductive success and survivorship of lynx. This correlation has been presented as evidence that snowshoe hare populations can be used as a surrogate of habitat capability for lynx. It can further be implied that an increase in snowshoe hares is likely to benefit other carnivores as well. Similarly, habitat capability for large ungulates has been postulated as a surrogate of habitat quality for wolverines, and distribution of microtines as a measure of habitat quality for marten. These kinds of interpretations can be dangerously incorrect.

Implications derived from correlations between predator and prey populations seem worthy of consideration, but they are very simplistic, and it must be recognized that many other factors contribute to habitat quality. For example, lynx-snowshoe hare relationships observed in the north are not applicable to western mountain habitats within the United States. As discussed by Koehler and Aubry (Chapter 4), the more southerly hare populations are not cyclic but instead should be considered similar to hare population lows in the northern boreal forests. Even if hare habitat were improved, it might prove detrimental to the predator. It is possible, for example, that conversion of late-seral components required for resting and denning by lynx into early seral hare habitat could prevent lynx from occupying these habitats. The interspersion of foraging habitats with habitats that address other life needs appears to be a requirement for all forest carnivores.

The assumptions regarding forest carnivores other than lynx require even more care and consideration because the potential for habitat loss seems almost as great as the potential for habitat improvement. Even if we assume that success in managing habitat to produce high hare densities might benefit fishers, we must also consider that any benefit will be limited by the degree to which patches of high hare density are accessible to fishers from adjacent resting and denning cover. In addition, the manager must consider whether habitat manipulation might result in increased snow depths. Reductions in tree canopy to increase herbaceous vegetation for hares could favor lynx, but where snow depths are also increased, fishers could well be excluded. Disturbance, including logging, can increase the abundance of small mammals, especially cricetine mice. However, marten prefer the voles and pine squirrels associated with mesic, late-seral habitats. Similarly, management to create early seral communities for ungulates might not provide adequate security for wolverines or sufficient den sites for marten or fisher.

Stand Management to Benefit Forest Carnivores

The potential for short-term direct action to manipulate hunting habitats to favor predation by marten, fisher, and lynx seems somewhat limited. Removal of canopy often affects these species adversely, depending on the scale of canopy removal. One possible exception was suggested in a dissertation where second-growth marten habitat appeared to be suitable because it included large-diameter coarse debris. Until this research has been confirmed in other

areas, we consider it doubtful that individual structural components, like residual material from late-successional stands, can meet marten habitat requirements. In the case of the wolverine, the creation or improvement of hunting habitat has not been attempted, and success seems highly unlikely considering the aversion shown by wolverines toward human activities.

Landscape Considerations

The preceding discussion has indicated stand-level requirements for denning, resting, and foraging by all four forest carnivores. Acceptable within-stand structural components for denning and resting appear to be somewhat comparable, but these features alone may not meet foraging requirements. Thus, while stand-level structures provide essential habitat components, stands must have suitable spatial distribution over a landscape if habitat needs are to be satisfied. Lynx usually select den sites connected by travel cover, or close to early successional forests where hares are abundant. This adjacency requirement seems more apparent for the lynx because there are obvious disparities between early-seral foraging habitat and late-seral denning requirements. However, the arrangements and linkages between stands are even more important for species like the marten and fisher that exhibit great reluctance to cross openings or venture very far from overhead cover. For these species, fragmentation of continuous forest cover may have negative consequences.

Home Range Habitats

Earlier in this discussion, we defined a landscape as an aggregate of stands large enough to encompass at least one average home range. We emphasize here that such a landscape, in a context applicable to forest carnivores, can be extremely large. Landscapes must provide all the stand attributes of habitat and, in addition, travel cover to connect the components. The home range is probably the minimum spatial unit capable of supporting a single individual. Home range size is not well described for any of the forest carnivores except marten, but all home range estimates are considered large in relation to the size of the animal. One important management consideration appears to be the relationship between home range size and tolerance for openings and fragmentation. The marten, with an average home range under 16 km^2, requires a very high level of habitat connectivity within that range. Fisher home ranges are at least twice as large, and while the fisher exhibits some tolerance for openings, forests fragmented with open areas are used infrequently by fishers. A lynx home range can be 6-8 times larger than the marten, but lynx habitat can be quite diverse and fragmented. The very large home ranges of wolverines (up to 900 kmz for males) seem to be less affected by fragmentation than by major dissection and human intrusion.

If a home range is viewed as the habitat unit required by a single animal, an initial management concern might be the size and spatial array of stands required for a suitable home range. Among the four forest carnivores, lynx appear to be the most tolerant of disturbed landscapes. Indeed, a basic requirement of lynx habitat may be an early successional component significantly greater than acceptable for the other species. Early successional forests resulting from fire or timber harvest provide conditions that favor snowshoe hares and which, in turn, benefit lynx. At the same time, lynx require cover for security, for stalking prey, and for denning. At the southern limits of their distributional range, the fragmented and discontinuous nature of available habitats are sometimes cited as the reason both hare and lynx populations are more stable (although less dense) than populations at more northern latitudes. Productive lynx habitat appears to consist of a mosaic of old and young stands, both dense and fairly open, with diversity in communities expressed on both spatial and temporal scales.

Landscapes with abundant early successional stands and small patches of mature forest are not likely to provide acceptable habitat for the other three forest carnivores. Fishers appear to require a high proportion of continuous and mostly mature forest. For marten, overhead cover is essential, and the habitat should probably be continuous. A diversity of communities and younger stands might conceivably be acceptable for wolverine, but the almost certain presence of human disturbances makes acceptance highly unlikely.

POPULATION MANAGEMENT CONSIDERATIONS

Landscapes and Metapopulations

Obviously, if a home range area is needed for a single animal, then multiple home ranges are required to support a population. For a species like the marten, several adjacent home ranges simply become a larger landscape; but for a wide-ranging species like the wolverine the population unit might be an

ecoprovince. In terms of habitat suitability, the size of the area is not as important as the concept that a population can only exist where landscapes adequate for individual home ranges are numerous and interlinked.

Habitat descriptions for landscapes adequate to support populations are virtually nonexistent. Buskirk and Ruggiero (Chapter 2) indicate that behavioral and population responses of marten to such landscape attributes as stand size, shape, interior, insularity, corridors, and connectivity are largely unknown. The same statement certainly applies to fisher and probably to lynx and wolverine, but at very different landscape scales.

The importance of scale cannot be ignored because our understanding of landscape configurations declines drastically for the species with larger home ranges. Habitat that provides for the life requisites of the marten and fisher and their prey may only provide for lynx and wolverine at the stand level, and while we have some appreciation of the landscape diversity required for lynx, our knowledge of wolverine habitat needs at the landscape scale is virtually nonexistent. Banci (Chapter 5) points out that if we do not know what wolverine need in habitats where their numbers are stable, it will be extremely difficult to provide for the needs of populations whose status is tenuous.

The implications of maintaining population-level habitats extends to maintenance of habitat linkages/corridors between possible population centers. Populations of marten, fisher, and lynx can be characterized by fluctuations in excess of an order of magnitude, influenced by spatial and temporal variation in prey abundance. It may even be perfectly normal for these populations to exhibit episodes of local extinction and recolonization. Thus, the maintenance of linkages within a larger metapopulation becomes significant as insurance against random local extinctions. The wolverine, on the other hand, occupies such an extremely large landscape that recolonization of vacant habitats may not be of as much concern as for other species.

Fragmentation and Linkages

Throughout the species chapters we see reiterated statements indicating that forest fragmentation is the most important isolating mechanism working today. Only the wolverine appears to be immune, and that may simply be a perception related to tremendous home ranges occupied. In any case, all the chapter authors agree that maintaining habitat linkages between populations may be important to ensure the long-term viability of isolated populations. Activities that fragment, dissect, and isolate habitats have undesirable effects on all forest carnivores in two different ways. First, disturbance in forest habitats attracts habitat generalist predators like the great-horned owl, coyote, and bobcat. All can be successful competitors, and the smaller forest carnivores can also become prey. Equally important, maintenance of habitat quality requires maintenance of linkages, connectedness, and interspersion over geographic areas large enough to benefit individuals and join individuals into populations. Newly isolated populations will be generated unless efforts are made to eliminate and reverse forest fragmentation.

Fragmentation in forest habitats is most frequently caused by human activities including road construction and logging. The amount of habitat disruption that can be tolerated is not known, but the negative impact appears stronger for marten and fisher than wolverine and lynx. Powell and Zielinski (Chapter 3) indicate that riparian areas appear to be important elements in marten and fisher home ranges and may be dispersal avenues. This is probably true for the other species as well, suggesting that protection of riparian corridors is a valid management concern. It is, however, unknown whether fishers will use corridors of forest through otherwise open habitats. Despite some exceptions in rural environments, none of these carnivores are likely to persist where people or human influences dominate the landscape.

Detecting Carnivore Populations

The forest carnivores considered here occur at low densities, are primarily nocturnal, leave little sign, and shun human activity. Unless they are commercially harvested by trapping, their presence can easily go undetected. Given these problems, an overriding initial management concern is to determine whether any of these species are even present. Where commercial harvest is permitted, information on the location of trapped individuals can answer this question. Where commercial harvest does not occur, a variety of techniques are available for attempting to detect the presence of these species. New approaches, such as the use of baited cameras, sooted track boxes, and traditional methods such as snow-tracking are useful, but protocols for the consistent application of these techniques are currently lacking.

Caution should be exercised in the interpretation of survey results. Failure to detect a species has multiple implications. Until standardized methods for detection are developed, the confidence in declaring "absence" will be low. And, even if failure of detection conveys a high probability of absence, the unstable nature of some forest carnivore populations suggests that areas of suitable habitat could be occupied in the future. Finally, because management activities occur in small areas, relative to the home ranges of some of the species considered here, communication with the managers of adjacent lands is essential. The existence of a population nearby indicates the potential for recolonization of currently unoccupied, but suitable, habitat.

Population Abundance and Trends

Although methods currently under development should allow managers to determine whether forest carnivores are present or probably absent in a particular location, methods of indexing or estimating population size are costly and have not been rigorously tested. Indeed, the detection of population changes at any measurement scale, ranging from presence /absence to ratio estimation, has not been shown to be feasible. The use of any of the detection methods, over time, may eventually become a successful means of indexing population change. However, before managers can evaluate the effect of trapping or habitat manipulation on populations of these species, a successful population monitoring protocol must be developed.

Population Dynamics and Habitat Management

The abundance and fitness of any forest carnivore population will be affected by habitat quality and by community interactions that may be mediated by habitat. As already noted, some populations may never be stable in an area, due to factors independent of their specific habitat needs (e.g., variation in abundance of prey, competitive interactions with other carnivores, time lags in recolonization). While this may suggest that habitat management is superfluous, that is not the case. Although suitable habitat may be a necessary but not sufficient requirement for healthy populations, habitat manipulation is the primary method by which forest managers influence forest carnivore populations.

The Effects of Trapping

Commercial trapping can affect populations and habitat management in several ways. Our attempts to manage furbearer populations hinge on the assumption that there is a positive relationship between populations and habitat quality. Thus, human-induced mortality that exceeds natural levels, or that affects age or sex structure, can affect population persistence by influencing population response to habitat variation or by obscuring the relationship between habitat and populations. Efforts to enhance populations via habitat management will be less effective if trapping reduces the population or changes the relationship between population density and habitat quality. Trapping can also induce behavioral changes in individuals that can affect habitat choices. And, if trapping eliminates adults, which are usually considered to make habitat choices with the benefit of the greatest experience and with the fewest social constraints, it cannot be assumed that trapped populations will exhibit the same use of habitats and home ranges as unexploited populations.

A frequent objective of a trapping program is to reduce the variance in population size, yet this natural variance is what provides the impetus for dispersal and recolonization. Even moderate trapping levels can affect the dynamics of populations. For example, if dispersing individuals are essential to maintain metapopulation integrity and to recolonize locally extirpated areas, trapping may eliminate potential emigrants and slow recolonization. This can be especially critical where refugia have been established as a part of a management program for wolverine, lynx, or fisher. A failure of coordination between political jurisdictions can also result in overexploitation that decreases the number of emigrants.

Trapping programs can be compatible with the conservation of forest carnivores, especially in the northern extent of their range, if they are managed to be sustainable. Sustainability can be enhanced if adults are minimized in the harvest, seasons are timed so that females with dependent young are not killed, and trapping mortality occurs during a season when most natural mortality occurs. Banci (Chapter 5) has suggested that jurisdictions that do not have the resources to monitor populations at the level of intensity required, or do not have large refugia, cannot justify a harvest. Although the land manager has little authority to regulate commercial harvest, the issues summarized here highlight the interaction between fur trapping and habitat management.

Finally, it should be emphasized that where sustainable harvests can be defended, managers can reap important information benefits from responsibly managed commercial harvest programs. Caution must be applied when using fur harvest data to interpret population parameters, but careful documentation of trapping effort and trapping locations can provide a source of information on population distribution and possibly indices of abundance.

SPECIES MANAGEMENT CONSIDERATIONS

All four forest carnivores considered here have suffered range reductions in historic times. Trapping and habitat destruction have been individually and jointly implicated. However, development of a conservation strategy for these species will require a far more complex analysis of habitat loss and trapping influences than has so far been developed. With the possible exception of the marten, these forest carnivores occupy extremely large geographic areas to maintain populations of low absolute density. This situation has implications that must be recognized across adjacent ecoprovinces and geographic regions for both habitat management and population management.

Managers must begin to think about ecosystems in which forest carnivores coexist and interact with a common prey base (see Chapter 7 for further discussion). Ecosystem management will be essential for forest carnivore conservation, but the concept must be built upon knowledge of each species' ecology and upon broad landscape-level planning. Relevant scales for each species need to be integrated. The challenge is to determine how the scales overlap for all four species and how this information can be used to better manage the ecosystems in question.

Regional Management

Our knowledge of species ecology suggests that forest carnivore management should be developed at the regional level, rather than provincial or state administrative levels. Indeed, Banci (Chapter 5) suggests that evaluation of the population status for wolverine requires a multiregional scale. If habitats and populations are to be reasonably connected, it is necessary to plan landscapes at the species level, which means a great deal of cooperation among adjacent management jurisdictions. The U.S.-Canadian border, for example, includes 15-20 administrative and jurisdictional authorities that may influence management of transborder wolverine, lynx, and fisher populations. Clearly, if a conservation program is to benefit forest carnivores, it must transcend political boundaries. And, in the same way, if refugia and protected habitats are to function as population sources, coordinated management with common goals and objectives is a necessity.

Reintroduction

Where populations have been extirpated, reintroductions into areas of suitable habitat may be appropriate. Before such management strategies are implemented, however, it is essential that the causes of extirpation be evaluated to determine if reintroduction is likely to succeed. Local extirpations are usually due to the combined effects of overtrapping, loss or degradation of suitable habitat due to timber harvesting, and disturbance from human encroachment into wilderness areas. Unless these conditions have been remedied, there is no logical justification for considering reintroduction. Suitable habitat must be restored before reintroduction can succeed.

Ecotypic factors must also be considered. Genetic and behavioral differences may exist among metapopulations, and animals from one geographic region may not be suited for survival in a different region. If remnants of the population are still present in the target area, the introduction of genetic stock from other areas may swamp existing populations with maladaptive genes. This phenomenon, known as "outbreeding depression," has physiological effects and population implications similar to those described for inbreeding depression. Further, even if genetic differences among populations of forest carnivores are not significant, the acquired behaviors of individuals may influence the success of reintroductions. Individuals that have existed in one forest type with a particular structure and array of potential prey may have difficulty surviving in a substantially different forested environment, especially in the critical period immediately following release. Thus, animals selected for reintroduction should be from the same metapopulation or ecotypes as once occurred in the target area, or at least from forested habitats similar in structure and species composition.

Existing Populations

The primary objective in the conservation of forest carnivores is to prevent the decline and extirpation of extant populations. All four species have their

distributional centers in the boreal forests of northern North America. Populations in montane regions in the western United States, including the Rocky Mountains, Cascade Range, Olympic Mountains, Coast Ranges, and Sierra Nevada, represent southern extensions of these ranges. Those populations at the southernmost limits may occupy marginally suitable habitats. These are also the areas in which human encroachment into otherwise suitable habitat tends to be the most severe. Boreal habitats in montane regions are peninsular in nature, and populations in these regions are much more likely to become fragmented and isolated from each other than are populations in the north. Range reductions for all four species have occurred in the western mountains, and for marten and fisher in the northeast; all have been either at the southern margin of species' distributions or in peninsular extensions of continuous distributions in northern boreal regions. Management concerns will be greatest in these areas.

Fishers are not good colonizers of isolated patches of suitable habitat and marten have relatively small home ranges and low dispersal capabilities. Thus, small, isolated populations of these species may be particularly susceptible to extirpation resulting from stochastic demographic or environmental events, because recolonization of these areas may not be possible. Local extirpations from portions of a species' range results in the further isolation of remaining populations.

In California, two populations of fishers may be effectively isolated; one in the southern Sierra Nevada and another in the northwestern part of the state. Because fishers appear to be very rare in Oregon and Washington, especially in the Olympic Mountains, fisher populations in California may be completely isolated from those in Canada and the eastern United States.

Marten also occur in isolated populations in the southern Rockies and Pacific States. Marten are found in very low numbers in the Olympic Mountains in Washington and are apparently isolated from populations in the Cascade Range; marten are rare or extinct in the Coast Ranges in southern Washington and in Oregon. The status of the Humboldt marten (*Martes americana humboldtensis*) in northwestern California is also uncertain.

Wolverine have declined dramatically in the western United States in the last 100 years but are apparently beginning to recover in certain areas. The wolverine is a boreal forest and tundra species that occupies habitats near treeline in the western mountains. Thus, even in areas where wolverine occur in the western mountains, gene flow may be restricted by the disjunct distribution of preferred habitat. Thus, for wolverine, as for fisher and marten, the western montane regions are of particular conservation concern.

Lynx have been extirpated from Oregon and occupy only the northernmost portions of the Cascade Range in Washington; they also occupy a relatively narrow distribution in the Rockies. Montane habitats appear to provide less productive but more stable habitat for lynx, probably because snowshoe hare populations do not cycle to superabundance in montane forests as they do in the northern boreal forests.

The implications of these population declines for conservation are not clear because they have not been studied through time. At the same time, we do know that every one of these forest carnivores is considered sensitive, threatened, or extinct in one or more of the western states, on one or more of the national forests, or in some part of its range by the federal government. Nothing in our review of existing knowledge suggests that conservation status designations by these agencies are incorrect. The state of existing knowledge makes it clear that concern about the conservation of forest carnivores is justified.

CONCLUSIONS: THE MAJOR CONSIDERATIONS FOR MANAGEMENT

In this section, we bring together and emphasize those overarching considerations that appear to be important in any situation where one or more of these forest carnivores might occur.

- We found nothing in our assessment to suggest that existing designations of forest carnivores as species of concern are incorrect. We conclude that conservation strategies for forest carnivores in western mountains are needed to ensure their persistence.
- Complex, large physical structures commonly associated with mesic late-successional forest stands will be important in forest carnivore conservation. There is little information to suggest that forest carnivore habitat requirements can be met by these components outside of their natural ecological context.
- Research in forest carnivore ecology produces information that can be used to design silvicultural prescriptions. Monitoring species' response following management actions cannot adequately meet this information need.

- Habitat modification that favors generalist predators is potentially detrimental to forest carnivores.
- Further reduction or fragmentation of late-successional forests, especially through clearcutting of contiguous forest, may be detrimental to the conservation of forest carnivores. This may be most true for marten and fisher, and specific effects will depend on the context within which management actions occur.
- Forest carnivore conservation will require an ecosystem management approach at the landscape scale. Management at the scale of the stand will not suffice for conservation.
- Interregional, interagency, and international cooperation will be essential to conserving forest carnivores.
- Maintaining ecotypic variation in forest carnivore populations, including those on the periphery of a species' range, may be crucial to forest carnivore conservation.
- Special conservation challenges exist where isolated populations are identified.
- Major information gaps exist for these forest carnivores. A sustained commitment to research is needed for developing scientifically sound conservation strategies to ensure the persistence of forest carnivore populations.
- Although there is insufficient information available to develop highly reliable conservation strategies, this should not deter management from developing conservative interim guidelines that will maintain future options.

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Chapter 7

Information Needs and a Research Strategy for Conserving Forest Carnivores

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INTRODUCTION

This forest carnivore conservation assessment summarizes what is known about the biology and ecology of the American marten, fisher, lynx, and wolverine. It is the first step in ascertaining what information we need to develop a scientifically sound strategy for species conservation. Although this assessment implies that we know what information we need to prescribe necessary and sufficient conservation measures, the concepts of conservation biology used here give us a better basis for identifying "necessary" information than for identifying "sufficient" information. Thus, we are cautious in defining information needs for the development of conservation strategies.

In this chapter, we define the categories of information that are prerequisite to developing conservation strategies. We then discuss conceptual issues that relate to design and the reliability of research results within each category. We do this not only as a basis for our research recommendations, but to provide the reader with information for use in evaluating available literature and, hence, our existing knowledge base. For each category of needed information, we also present specific information needs, provide a rationale for each need, and identify commonalities among species when possible.

Research that addresses information needs usually cannot be generalized for the entire range of a species. Populations within species may be unique in their genetic or acquired attributes, thus representing important elements of variability that must be maintained as part of any sound conservation strategy (see Chapter 5 for additional discussion). Such variation occurs as ecotypic adaptations to the different environments inhabited by populations throughout the range of the species. It follows that the range of behavioral variation exhibited by a species is not necessarily the same as the range of behavioral variation exhibited by populations within species. Thus, it is inappropriate to attribute the characteristics of a widely distributed species to any given population. It is therefore ecologically naive and risky to generalize the results of studies conducted in one portion of a species' range to much different environments in other portions of the range.

One solution to this problem is to define land units that may influence behavior and population phenomena in some consistent and potentially unique fashion. Such a land stratification must be based on ecologically important characteristics (e.g., physiography, vegetation, and climate). We have adopted the classification scheme of Demarchi (Appendix A) for this purpose, and we use this framework to define

land units within which studies should be replicated in order to make geographically relevant and scientifically reliable inferences about populations.

The following categories of information needs are addressed in this chapter: habitat requirements at multiple scales; community interactions; movement ecology; population ecology and demography; and behavioral ecology. In our discussion, we emphasize *populations* as the appropriate level of ecological organization for making scientific inferences about habitat requirements (for reasons discussed above and in Ruggiero et al. 1988). However, such inferences are based on research designs that sample the responses of individual animals within available habitats. Thus, our references to the habitat requirements of populations and species are predicated on sampling the range of variation in the habitat selection patterns of individuals.

In all cases, our use of the term "habitat" refers to a vegetation community without implying use by the animals in question. We use the term "stand" in the context of habitat for highly mobile carnivores, and, by definition, a stand is always smaller than a home range for any of the species in question. Finally, we define the term "landscape" to denote a geographic area approximately equal in size to *x* times the median home range size for males of the species in question. Thus, landscapes are not fixed entities; rather, they are defined relative to the mobility of the species in question. For analytical purposes, landscapes are to be nested within ecologically meaningful bounds (e.g., physiographic features corresponding to watersheds) whenever possible.

OVERVIEW OF EXISTING KNOWLEDGE

Most of what we know about forest carnivores (table 1) is based on studies conducted in Canada or Alaska (wolverine and lynx) or in the eastern United States (fisher). Relative to the other forest carnivore species, we know the most about marten ecology in the western United States.

Most of the publications reported in table 1 addressed multiple topics. Thus, the total number of publications (roughly equivalent to independent studies) is small relative to the total number of publications shown in the body of the table for each species. Our knowledge base is more a product of the number of independent studies than of the number of topics addressed per study. With this in mind, an examination of table 1 reveals that our knowledge base for developing conservation strategies for forest carnivores in the western United States is extremely limited. Examination of the summary tables presented in each species chapter reveals that our entire knowledge base on wolverine ecology in the western United States comes from one study. The comparable number for lynx is five and for fisher, four. Moreover, some of the publications listed in table 1 resulted from studies that were conducted on the same study area at different times by a series of investigators, often graduate students. Thus, much of the knowledge we have is a product of relatively short-term research conducted by inexperienced scientists with modest amounts of money and field assistance. This situation adds to concerns about the nature of our existing knowledge base when one considers that forest carnivores are rather long-lived and studying them is extremely labor-intensive.

INFORMATION NEEDS

Information needs are a function of extant knowledge, and we have a great deal to learn. We describe the information needed to develop conservation strategies in the following sections. Our recommendations about information needs are based on the expert opinions of the species-chapter authors and on our interpretations of the existing scientific basis for species conservation as presented in the species chapters and elsewhere. The amount of detail we provide in identifying these needs varies among information types and reflects the state of knowledge; relatively well-developed areas of knowledge permit us to be more specific about information needs than do areas where knowledge is more poorly developed.

Habitat Requirements at Multiple Scales

We define habitat requirements as elements of the environment necessary for the *persistence of populations* over ecologically meaningful periods of time (Ruggiero et al. 1988). For the conservation of forest carnivores, habitat requirements must be described in terms of the kinds, amounts, and arrangements of environments needed to ensure population persistence. This set of conditions should be described at multiple ecological scales and for all geographic areas of concern.

Conceptual Issues

Patterns of habitat use are generally used to assess habitat requirements. However, patterns of use may differ when considered from different spatial or temporal perspectives. As examples, patterns of habitat use may vary as environmental conditions change over time (temporal perspective), and the spatial context within which stands occur may reveal crucial information about the use or non-use of stands (spatial perspective). Because of this, we emphasize issues of scale and spatio-temporal variability in habitat relationships. Failure to address or account for such variability can undermine the reliability of research results. Accordingly, questions about kinds, amounts, and arrangements of environments required by populations and species should be asked at the stand, home range, landscape, physiographic province (e.g., ecoprovince), and regional scales and in the context of seasonal, yearly, and longer time frames. Some combinations of these factors (e.g., habitat amounts at the regional scale viewed in the context of seasonal variation) may be less important than others, but we still must contend with a complex set of considerations when asking questions about habitat requirements.

Habitat Kind(s).-The kinds of habitats required by populations and species refers primarily to vegetation communities (in some ecological context) and their associated structural and compositional attributes. At the stand level, information is needed about the kind (type) of vegetation community represented and its structural and compositional char

Table I.--Numbers of publications of original data dealing with free-ranging forest carnivores in North America, by subject and area. Theses and dissertations are not considered separately from publications and final reports that resulted from them, so that each publication equates with a single data set on that species and subject. A single publication may be represented in more than one category. Agency final reports and general technical reports that are widely available are included. Publications dealing with parasites and diseases were excluded except when implications for species conservation were discussed. (n.a. = not applicable)

	Marten	Fisher	Lynx	Wolverine
Food habits				
Western	14	3	2	1
Eastern	1	12	0	n.a.
Alaska	2	n.a.	0	4
Canada	13	7	10	1
Habitat				
Western	20	5	2	1
Eastern	6	6	0	n.a.
Alaska	2	n.a.	1	3
Canada	14	6	1	2
Population ecology, general				
Western	8	1	1	1
Eastern	2	7	1	n.a.
Alaska	0	n.a.	5	3
Canada	6	2	9	2
Demography				
Western	8	1	1	0
Eastern	2	7	1	n.a.
Alaska	0	n.a.	4	3
Canada	5	3	7	1
Reproductive biology				
Western	5	3	1	1
Eastern	1	7	0	n.a.
Alaska	0	n.a.	3	5
Canada	3	1	1	2
Movements				
Western	6	4	1	1
Eastern	1	10	1	n.a.
Alaska	1	n,a.	0	3
Canada	6	4	5	2
Home range				
Western	7	3	4	1
Eastern	7	4	1	n.a.
Alaska	3	n.a.	3	3
Canada	9	1	6	1
Prey relationships				
Western	2	0	1	0
Eastern	0	3	0	n.a.
Alaska	0	n.a.	2	0
Canada	2	0	3	0
Community interactions				
Western	2	0	2	0
Eastern	0	3	0	n.a.
Alaska	0	n.a.	1	1
Canada	4	2	3	3
Trapping effects				
Western	1	0	0	0
Eastern	1	0	0	n.a.
Alaska	0	n.a.	1	0
Canada	1	0	1	0
Total publications				
Western	33[2]	9	6	1
Eastern	11	20	2[1]	n.a.
Alaska	3	n.a.	5	8[1]
Canada	21	10	14	5

[1]*One of these publications also reported data from Canada.*
[2] *18 of these publications are M.S. theses or Ph.D. dissertations.*

acteristics. At the home range and higher scales of spatial consideration, the same information is needed for the entire range of vegetation communities used by the target animals and subsumed by the spatial scale in question.

Habitat Amount.-The amount of habitat required by populations and species refers to the quantitative description of the habitats in question. At the stand level, these measurements should include total area and quantification of the structural and compositional characteristics of the stands. At spatial scales of home range and above, the range of values for structural and compositional attributes is needed for each habitat type along with measures of the composition of the area in question relative to the habitat types thought to be important to the target animals.

Habitat Arrangement.-The arrangement of habitats required by populations and species refers to the pattern of environmental features at all spatial scales. At the stand level, this includes measures of the distribution of structures by type (e.g., logs), size, and other attributes of interest. At spatial scales of home range and above, we need to quantitatively describe spatial relationships (juxtaposition, etc.) among habitats and to describe landscape attributes (e.g., measures of fragmentation) that result from such arrangements. Considerations of habitat arrangement at the home range level and above must include measures of relative use of habitats. These measurements give a sense of how the amounts and arrangements of all *available* habitat types affect dependent variables like variation in home range size, variation in vital rates, and general patterns of occurrence.

Reliability and Utility of Information

Ecological relationships that define and influence habitat *requirements* (i.e., resources or environmental features without which a population would become extinct over a given time frame) are complex and difficult to quantify because they are dynamic in time and space, modified by biotic and abiotic factors, and subject to the influence of human activities. For these reasons, the identification of habitat requirements involves exceedingly complex and challenging research problems. For all practical purposes, because of limitations in time and resources available for research, precise information about habitat requirements is unattainable. However, the probability of population persistence is primarily a function of how well animals in that population are adapted to their environment or, for the purposes of this discussion, their fitness.

Ecologists use various indirect measures of fitness when attempting to understand and elucidate habitat requirements. Unfortunately, the reliability and utility of these measures is variable. Moreover, inappropriate measures and inadequate interpretation relative to theory can lead to marginally useful and even misleading results (McCallum, in press; Ruggiero et al. 1988). Relative fitness values among populations occurring across a range of available environments can be most reliably estimated in terms of each population's size, structure, and age-specific reproductive and survival rates. In the following discussion, we address different measures of habitat association and their merits relative to understanding habitat requirements.

Presence/Absence.-Data on presence/absence of animals in habitats can be used to establish habitat use under some circumstances. However, the existence of an animal in some environment at one point in time says little about what the individual requires for survival or what the population requires for persistence. Accordingly, presence/ absence data is, by itself, unreliable as the basis for inference about habitat requirements.

Relative Abundance.-Data that estimate and compare abundance in different habitats is subject to biases inherent in sampling (detecting, counting) individuals under the different conditions associated with each of the habitats being sampled. Although measures of relative abundance can be used to rank habitats according to *use*, these measures are subject to some of the same limitations as presence/absence data in that they say nothing about the habitat conditions required for population persistence. And without associated measures of sex and age structure, recruitment, and survival, it is impossible to know if high relative abundances indicate optimal or suboptimal habitats. Because this distinction is crucial to inferences about habitat requirements, relative abundance data as an indicator of habitat requirements are only slightly more reliable than are presence/absence data.

Density.-Density estimates are subject to most of the same limitations as are relative abundance estimates. The advantage of density estimates is that they provide an absolute rather than a relative measure of habitat use. This distinction is useful for estimating carrying capacity, but only under the conditions extant at the time of sampling because densities are sensitive to short-term changes in environmental conditions. As with relative abundance estimates,

density estimates can be misleading because suboptimal habitats can have higher densities of individuals than optimal habitats (McCallum, in press; Van Horne 1983).

Preference.-Habitat preferences can be inferred based on statistical analysis of data on habitat use and habitat availability (Neu et al. 1974), but interpretation of such analyses can be incorrect if they are not made with full consideration of all the factors that influence occurrence patterns of animals. These factors (e.g., saturation level of habitat for territorial species, absolute length of available habitat gradient) can confound the interpretation of occupancy patterns resulting in erroneous conclusions (McCallum, in press). For example, an abundant habitat may be used less than expected based on availability, and this can lead to the conclusion that the habitat is avoided. But the habitat in question may be vital to species persistence as is the case with closed canopy forests and grizzly bears in Yellowstone National Park. As another example, elk often use closed logging roads as bedding sites and, because such sites occupy a very small portion of the total available habitat, use vs. availability analysis may predict that road surfaces are a preferred habitat component for elk.

Erroneous conclusions may result in management actions that could contribute to population decline. For example, habitat preferences are constrained by habitat availability (i.e., animals cannot select habitats that are not available to them). Because of this constraint, preferred habitats may represent the best that is available while failing to represent environments necessary for population persistence. Failure to recognize this when it occurs can result in a description of "habitat requirements" that will not meet the long-term needs of the population/species in question. This failure can have catastrophic consequences when the resultant habitat descriptions become the goal for habitat modification through management. Management actions that are so guided can become the basis for widespread habitat modification that is antithetical to species conservation. Habitat preferences, when carefully interpreted, can serve as reliable estimates of fitness levels in different habitats (McCallum, in press; Ruggiero et al. 1988). However, the most reliable way to estimate fitness, and hence describe habitat requirements, is to measure population performance across the range of available habitats.

Population Performance.- The quantification of population performance is crucial in defining habitat requirements because performance is a direct measure of how well-adapted populations are to the range of environments available to them. And, in turn, this is indicative of the probability of population persistence. Hence, direct measures of population performance provide the most reliable basis for assessing habitat requirements. This is done for populations with data on sex and age structures and vital rates that pertain to birth and death (Van Horne 1983). However, this is not a trivial exercise. For highly mobile, sparsely distributed species like those being considered here, effective (reliable) measurement of population performance across the range of available environments entails tremendous investments of time (long-term studies are necessary) and money (studies are very labor-intensive). Although some question the feasibility of this undertaking, reliable estimates of vital rates are essential for mathematical models that address population persistence. So, reliable, habitat-specific measures of population performance are fundamental to the development of conservation strategies even when reliable but more indirect estimates of fitness (e.g., preference) are available.

Studies Based on Experiments.-Carefully controlled experiments represent perhaps the most reliable of scientific methods (Romesburg 1981). However, experiments designed to deduce habitat requirements are not feasible at the spatial and temporal scales required for forest carnivores. Moreover, issues of experimental control, replication, and effects on sensitive populations all detract from the experimental approach (Ruggiero et al. 1988).

Specific Information Needs

1. There is a need for broad-scale correlative studies of forest carnivore distributions and habitat attributes that may explain their presence or absence. This will provide additional information about species distributions and habitat associations, while allowing us to pose hypotheses that can be tested at smaller scales.

2. For the wolverine and lynx, and for the American marten and fisher in the Pacific Northwest, there is a need for the most basic information on habitat relationships, at any spatial or temporal scale and at any level of measurement. Virtually any new data on habitat relationships involving wolervine and lynx in the western conterminous 48 states would be a substantive increase in knowledge. We particularly need knowledge about how these species use forest successional or structural stages.

3. We need to understand how forest carnivores use habitats at spatial scales above and below those that have been most commonly investigated. For martens, fishers, and lynx, these include use of edges, small nonforested openings, patch cuts, and gaps in the canopy caused by the death of individual trees. Pursuing this goal will require gathering data that have small measurement error relative to the size of the feature being studied (e.g., when studying edge use, animal locations must be accurate within a few meters).

For all forest carnivores, this includes the need for information on habitat within landscapes and larger areas. This includes such attributes as insularity, connectivity, and use of corridors. The need for consideration of temporal scale refers to the need to consider short-term habitat choices in explaining the proximal causes of habitat selection. Also, we need better characterization of seasonal and among-year variation in habitat relationships. This will enable us to identify which seasons are most resource-limiting for forest carnivores and the importance of episodic resource shortages in shaping short-term behaviors.

4. For all forest carnivores, we need better information on how sex, age, and social structure affect habitat choices. This information is important in explaining how habitat choices of individuals may be constrained by non-habitat factors.

5. In order to place habitat use by forest carnivores into the context of source-sink theory, we need better information on how habitat quality gradients affect dispersal rates, directions, and distances. This has important implications for our understanding of the factors that affect dispersal and metapopulation structure.

6. We need better knowledge of how forest carnivores respond to human-altered landscapes. We require specific knowledge of their responses to timber cutting, roading, clearing for seismic lines, and ski areas and development.

Community Interactions

Community interactions include competitive, predator-prey and other kinds of interactions among forest carnivores and between forest carnivores and other animal species. Information on these topics provides insight into how other animal populations mediate or confound the relationship between forest carnivores and habitat. The interactions included in this category range from the predation typical of forest carnivores, to killing of forest carnivores by other species because of habitat alteration, and to modification by other species of microhabitats that are important to forest carnivores.

Conceptual Issues

The availability of vertebrate prey and carrion is a major determinant of the distribution and abundance of forest carnivores. For fishers, lynx, and wolverine, almost no data are available on diets in the western conterminous 48 states, making informed discussion of their life needs difficult. Factors that affect availability of forest carnivore foods include abundance of snowshoe hares for fishers and lynx (see Chapters 3 and 4) and physical structure near the ground, which is used by martens to gain access to small mammals in the subnivean space (see Chapter 2). Physical structures near the ground may be also be important relative to the hunting behavior of fishers. For wolverines, sympatric ungulates and large predators that make carrion available are important in winter (see Chapter 5). Some of these prey availabilities are mediated by habitat (directly influenced by habitat conditions), others are not.

Generalist predators have been implicated in the deaths of martens and fishers (Clark et al. 1987; Roy 1991). Failure to assess the importance of changes in generalist predator populations and forest carnivore mortality rates as a result of landscape modification could lead to erroneous conclusions about the overall effects of habitat change on forest carnivores.

Some forest carnivores have resource needs similar to those of other forest carnivores and nonforest-carnivore species. For example, heavy use of snowshoe hares is made by fishers, lynx, and goshawks (Doyle and Smith, in press; Mendall 1944). This may result in competition among two or more of these species and confound interpretation of the effects of human-caused habitat change.

Forest carnivores have important non-predatory commensal relationships with other community members. These include the modification of microhabitats important to forest carnivores by other species (Chapter 2). Understanding these relationships will give us improved knowledge of the mechanisms underlying forest carnivore-habitat relationships.

Specific Information Needs

1. We need the most basic descriptive information about diets of fishers, lynx, and wolverines in the

conterminous 48 states. This information is needed on a seasonal basis and for different geographic areas. It also is needed in relation to supra-annual variation in food availability, especially for lynx.

2. For martens, there is a need for better understanding of how differences in prey *availability* affect habitat occupancy by martens. This is somewhat greater than the need for descriptive information on diets.

3. We need better information on how altered landscapes affect densities of generalist predators, such as coyotes and great-horned owls and, in turn, survival and behavior of forest carnivores. This information need relates especially to martens and fishers. It is important in understanding the mechanisms whereby habitat change impacts forest carnivores.

4. There is a need for better information on how competition for resources (e.g., prey) with other species (e.g., goshawk) may limit populations of forest carnivores. This need relates to all forest carnivores and may be important in explaining variation in survival and reproduction of forest carnivores.

5. For lynx, fisher, and marten we need to examine foraging efficiency across a range of seral stages and landscape configurations (e.g., edges, openings, juxtaposition of seral stages).

Movement Ecology

Movement ecology includes migration, dispersal, attributes of home ranges for animals that establish them, and movements beyond the home range relative to landscape features such as corridors. Home range information provides insight into the spatial organization of populations and how cohorts interact. Information on movements outside the home range provides insight into (1) the relationship of forest carnivore populations to each other and to landscape-scale habitat features, (2) the colonization abilities of each species, and (3) the survival implications of long-distance movements.

Conceptual Issues

Dispersal is the mechanism whereby juvenile forest carnivores locate vacant suitable habitat in which to live and reproduce. Emigration is the mechanism whereby resident adults attempt to locate new home ranges when forced to abandon old ones (Thompson and Colgan 1987). Thus, dispersal and emigration are the mechanisms by which geographic ranges are enlarged, new habitat is colonized, and metapopulations are maintained. Dispersal is successful only when individuals survive, establish new territories, and reproduce. Long distance movement is not the equivalent of successful dispersal, and movements per se do not reliably indicate dispersal capability.

Home ranges are the spatial units of organization of forest carnivore populations. Home ranges also are intrasexual territories for adults and are generally regarded as containing amounts of resources that ensure survival and reproduction of occupants. However, habitat fragmentation may result in increasing home range size beyond some upper energetic threshold, with further implications for survival and reproduction (Carey et al. 1992). Home range sizes and shapes are commonly used as a basis for estimating population density of forest carnivores, but the assumptions underlying this application of home range data are seldom stated and have not been tested. Density estimates are central to calculating total population size and to the parameterization of population persistence models.

Migrations by forest carnivores, although seldom reported in the scientific literature, could result from drastic among-year fluctuations in prey conditions and may function similarly to dispersal. Movements relative to landscape features (physiography, habitat quality gradients) will be affected by the connectivity of habitat, an important consideration in landscape design.

Specific Information Needs

1. We need basic information on the timing, frequency, and distances of dispersal and migration by forest carnivores. This includes the sex and age of animals undergoing long-distance movements and whether they become successful colonizers. This information is needed to determine which forest carnivore populations are isolated and to develop a conservation strategy for each species.

2. We need information on the importance of dispersal from Canada in maintaining numbers and geographic ranges of wolverines, lynx, and fishers in the Pacific Northwest and Rocky Mountains of the United States.

3. Better information is needed on how movements of forest carnivores are affected by habitat quality gradients and landscape-scale features. This includes the need for information on how survival of animals undergoing long-distance movements is affected by habitat attributes at various scales.

4. We need information on the relationship between home range size and habitat attributes, such as forested area in specific successional or structural stages. To manage forested landscapes for forest carnivores, we need better knowledge of how home range size and composition varies as a function of habitat attributes, such as those involving amount of forest interior and edge and stand connectivity.

5. To evaluate the precision of estimates of population density based on home range attributes, we require information, by sex, on how habitat is saturated with home ranges. This will allow us to generate variances associated with population estimates based on home range sizes. We can then generate confidence intervals around population estimates.

6. We need knowledge of whether and how forest carnivores use narrow corridors of various habitat types for movements beyond the home range. This is especially true of corridors along riparian zones.

Population Ecology and Demography

Population ecology refers to information about the distribution and abundance of forest carnivores at various measurement scales (e.g., occurrence, relative abundance, density) and various spatial scales. It comprises population indices, sizes, and trends; population genetics; metapopulation structure; ecological influences on survival and reproduction; and direct human impacts on populations. Demography refers to the sex and age structure of populations as well as to vital rates. These information types are essential to the management of harvested populations, to assessments of the effects of habitat change, to assessments of conservation status, and to the development of conservation strategies.

Conceptual Issues

Forest carnivores are shy, and populations are difficult to monitor, especially at higher measurement scales. As a result, the status of forest carnivore populations is not well known. This is especially true at the distributional limits of all four species and for the three larger forest carnivores, fisher, lynx, and wolverine, which occur at low densities even under optimal conditions.

Changes in distribution are difficult to detect if the reliability of data varies markedly over time or space (Gibilisco 1994). In such cases, important distributional losses may go unnoticed or stable distributions may appear to have changed. This is a particular problem with forest carnivores, which can require special efforts to monitor, even for presence/ absence data. Commercial trapping tends to make distributional information readily available. In cases where trapping has been discontinued because of scarcity of forest carnivores, perceptions of abundance of forest carnivores may change if agency efforts do not replace the lost data. Similarly, the absence of forest carnivores from an area is difficult to demonstrate because absence cannot be proven (Buskirk 1992; Diamond 1987). This is one reason that inferences about conservation status, population insularity, and metapopulation structure of forest carnivores are indirect and equivocal.

Ecological influences on survival and reproduction of forest carnivores are only poorly understood. For wolverine, for example, we have almost no empirical data about how ecological factors influence individual or population performance, and this interferes with our ability to develop effective strategies for habitat management.

Likewise, the existence and conservation significance of metapopulations is poorly documented for forest carnivores and limits our ability to understand whether adjacent populations are isolated. The importance of dispersal to forest carnivores, in combination with natural and anthropogenic fragmentation of their habitats, suggests that our lack of knowledge about metapopulations is a serious barrier to developing conservation strategies.

An important use for metapopulation data is in implementing the refugium concept. Although advocated for the conservation of forest carnivores in Canada for several decades (deVos 1951, see Chapter 2 for other references), the parameters underlying its successful implementation in the western United States have not been proposed or tested. If the refugium concept is to be applied scientifically to the conservation of forest carnivores in the western United States, then most of the information needs identified in this section must be met.

The sex and age structures of forest carnivore populations are important for understanding many life functions and population processes. Specifically, the relationship of demography to habitat use is just beginning to be recognized (Buskirk and Powell 1994), and more studies that consider habitat preferences in light of demography are needed to understand how habitat choices of individual forest carnivores may be constrained by intraspecific interactions.

Efforts to monitor reproductive success now rely on counts of corpora lutea or uterine scars of pregnancy (Strickland 1994). The reliability of recruitment data for forest carnivores would be improved by better knowledge of how many implanted embryos survive to parturition and how many neonates survive to sexual maturity. These data currently do not exist.

Fur trapping can confound our interpretation of the effects of habitat on population size and structure, but this relationship is poorly understood. As a result, it is difficult to attribute scarcity of forest carnivores to one or the other of these factors. The effect of habitat change on fur harvests has been little studied, as has the effect of artificial reduction of population size via trapping (Powell 1994) on how forest carnivores may be limited by habitat-mediated resource limitations.

Models of population persistence require parameterization with data on vital rates and variances thereof. These data are available only in the coarsest form for forest carnivores. Therefore, projecting the future for isolated populations and preparing scientifically based conservation strategies could not be reliably done with current knowledge.

The factors that affect persistence of isolated forest carnivore populations are not understood. Attributes such as population size and demography and duration of isolation have been related to persistence only for American martens in the Great Basin in prehistoric times. As a result, the development of conservation strategies currently must rely on theory rather than empirical information.

The genetic attributes of forest carnivore populations are largely undescribed and information on genetic processes in small, isolated forest carnivore populations is wholely lacking. Therefore, an entire category of processes that affects persistence of small isolated populations is completely unknown for forest carnivores. Because some forest carnivore populations are isolated and forest carnivores generally occur at low densities, this lack of information on genetic processes is an important issue. Without better knowledge of the genetic attributes and processes affecting forest carnivores, questions regarding persistence of small, isolated populations can only be answered with untested theoretical models.

Specific Information Needs

1. Better methods are needed for monitoring forest carnivore populations at various measurement and spatial scales. This is important for assessing conservation status and for preparing conservation strategies. Better methods to determine presence/absence need to be developed and should include derivation of detection probabilities for animals known to be present in an area. Multiple estimates of population size are needed for each forest carnivore species to test the precision and accuracy of estimates and indices.

2. We need better information on genetic 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 among subpopulations.

3. We need information about the factors that affect persistence of isolated populations of forest carnivores. These factors include duration of isolation, population size and demography, and variation in these attributes. Extant populations (and extinct ones represented by subfossils) isolated from others by land or water, present an opportunity to examine these issues.

4. To parameterize models of population persistence, we require better knowledge of the vital rates of forest carnivores, and how these rates vary among individuals, ages, years, and geographic areas.

5. We need better understanding of reproduction in free-ranging forest carnivores, including pregnancy rates, natality rates, and juvenile survival in relation to density, demography, and resource availability. Likewise, there is a need to know how the loss of genetic variability that may result from persistently small population size affects reproduction in forest carnivores.

Behavioral Ecology

Here we refer to reproductive, exploratory, foraging, and predator-avoidance behaviors. Reproductive behaviors include courtship and mating behavior, the selection and use of natal and maternal dens, and other behaviors associated with maternal care. Exploratory behaviors include territorial maintenance and exploratory forays beyond home range boundaries. Foraging behaviors are those related to food acquisition. And predator-avoidance behaviors are those by which forest carnivores minimize risks of being themselves preyed upon. Information on these subjects is important in understanding various aspects of population dynamics and habitat use.

Conceptual Issues

The central conceptual issue for these behavioral data is the way in which the behaviors described above constrain or are constrained by energetic factors or the use of habitat at various scales. Copulation has not been reported to require special habitats for any forest carnivore and likely does not represent an information need. But energetic considerations associated with courtship, copulation, and rearing of young may have important implications for habitat quality. Natal and maternal dens have been shown to be in highly specific habitat settings for some forest carnivores, but it is not clear whether the need for these sites is more or less limiting than other habitat needs.

Foraging behaviors are highly specific to each forest carnivore, type of food, season, geographic area, and habitat type. Knowledge of the ranges of and limits to these behaviors is essential to understanding the habitat requirements of forest carnivores. For martens, physical structure near the ground is important for foraging. For other forest carnivores, snow attributes or ambush cover may be more important.

Because forest carnivores are fierce predators, their vulnerability to being themselves killed by other mammals or birds is often overlooked. But, martens and fishers and, to a lesser extent, lynx and wolverines, can suffer losses to other predators. Both martens and fishers have evolved avoidance behaviors for certain types of habitats (e.g., openings). These behaviors generally are attributed to selection against behavioral tolerance of lack of overhead cover. Regardless of their origin, these behaviors severely constrain habitat use, use of fragmented landscapes, and probably dispersal. These behaviors, and the factors that affect them, are essential to our understanding of habitat use from the microsite to the landscape.

Specific Information Needs

1. There is a need to know more about the natal den and maternal den requirements of forest carnivores. Specifically, we require knowledge of how denning habitats affect reproductive success, and whether these habitat needs are more or less limiting than habitat needs for other life functions. The same information needs apply to rendezvous sites for wolverines.

2. Knowledge of how prey *vulnerability* is affected by habitat type would allow reconciliation of differences between the distributions of forest carnivores and their prey. This is especially true of lynx and their predation on snowshoe hares, but it applies to other forest carnivores as well. We also need better understanding of how successional stages and associated structural attributes affect vulnerability of several prey species.

3. Predator-avoidance behaviors need to be more specifically described in relation to species, season, and geographic area to understand constraints on forest carnivore use of habitats. Better understanding of these behaviors would allow us to interpret habitat use patterns.

A COMPREHENSIVE APPROACH TO MEETING RESEARCH NEEDS

Although the preceding sections suggest that many studies are needed to acquire the information needed for developing reliable forest carnivore conservation strategies, this is not necessarily the case. We believe that four types of well-designed, replicated studies can address virtually all of the information needs identified in this chapter. Moreover, our recommended approach obviates the need to dwell on the relative priorities of specific information needs. This is because most needs are addressed more or less simultaneously in one or more of the four study types defined in this section. The opportunity to address information needs in this way results from a comprehensive, programmatic approach to research as opposed to a piecemeal and opportunistic approach. The latter case is typical due to the way research is usually funded and managed.

General Research Considerations

In this section, we discuss several important general research considerations that pertain to the quality of a study, regardless of the information need being addressed. We then refer to these considerations in a discussion of the four study types alluded to above.

Study Methods

Methods must be appropriate relative to specific study objectives. For example, radio-telemetry methods represent the state of the art for addressing objectives about animal home ranges and some aspects of habitat use within home ranges. However, the relative lack of precision in telemetry locations generally renders it a poor (but commonly used) method for addressing objectives about how animals use

structures within home ranges and how things like edges influence movement patterns. For these objectives, snow-tracking methods, for example, provide more reliable information and therefore are more appropriate. Note, however, that radio telemetry facilitates methods like snow-tracking and generally provides the opportunity to employ numerous other data-collection methods. Accordingly, telemetry is an appropriate basis for designing comprehensive investigations of forest carnivore ecology.

Study Duration

The length of a study must be adequate to accomplish stated objectives. It is of little value to expend resources on demographic studies if one cannot commit to the long-term effort required to reliably estimate vital rates and their associated variances. Similarly, studies intended to describe habitat requirements must be of adequate duration to quantify habitat occupancy patterns over a meaningful period of changing environmental conditions, with 3 to 5 years defining an absolute minimum. Misleading results can stem from generalizing short-term results to requirements for long-term population persistence.

Study Intensity

The intensity of sampling associated with a study must be appropriate for meeting objectives. Sampling is often more intensive than is necessary to address a stated objective but not intensive enough to address more difficult objectives. For example, small mammal trapping is commonly conducted at a level of intensity that far exceeds that required to address presence/absence or relative abundance objectives, while falling short of the intensity needed to reliably estimate densities. The result is that all effort in excess of that required to meet the first objective is wasted. Similarly, geographically extensive, low-intensity sampling is often preferable to high-intensity sampling over a relatively small area. For example, extensive sampling may be more appropriate than intensive sampling when addressing objectives about patterns of animal occurrence relative to landscape-level features of the environment.

Study Design

All of the above considerations relate to study design, but there are additional, more general design considerations worth mentioning here. Adequate *sample sizes* are fundamental to all good research. Without adequate sample sizes, quantitative analyses of data and statistical inference are impossible or inappropriate. For example, a radio- telemetry study of habitat selection based on one or a few individual animals is of little value regardless of the study's intensity or duration. Similarly, studies with impressive sample sizes but no *replications* in time and space are of limited value in generalizing findings to other locations and times. It is necessary to replicate studies within geographic areas of interest (e.g., ecoprovinces) such that the variability inherent in the area is described adequately enough to make statistical inferences to the entire area as opposed to the study areas *per se.* Although single studies are often inappropriately extrapolated, the risks associated with doing so are unacceptable when the conservation of vulnerable species hangs in the balance. Finally, the selection of appropriate study methods is of little value when *techniques* for applying the methods are inappropriate or poorly applied. Radio telemetry, for example, is of little value if field techniques (e.g., locating animals, accurately recording locations) and data analysis techniques (e.g., proper treatment of error polygons, choosing appropriate models) are inappropriate or poorly applied. Carefully written *protocols* for implementation of study design are important in this context. Well-documented protocols also permit study methods to be consistently applied in replicated studies or if research personnel change. Good protocols also provide the basis for testing the reproducibility of study results.

Recommended Studies

We believe that information needs required for the development of conservation strategies for forest carnivores can be met by replicating four types of studies for each species in designated ecoprovinces. The study types are (1) intensive radio-telemetry studies of home range, habitat use, and movement ecology, (2) studies to quantify vital rates as a means of assessing habitat requirements and parameterizing mathematical models of population persistence, (3) extensive studies of species occurrence relative to landscape features, and (4) ecosystem studies that examine prey ecology, vegetation patterns within landscapes, and community interactions (competition and predation) among carnivores. These four basic studies can provide the foundation for important ancillary studies that examine various aspects of behav-

ioral ecology. Ancillary investigations will be integral to the basic studies and will be accomplished with the same levels of money and workforce required to address only the basic studies. This is possible when the effort necessary to accomplish the basic studies in a given location results in an effort adequate to accomplish the other essential objectives. A brief description of each study type follows.

Intensive Telemetry-based Studies

This type of study is based on the use of radio telemetry and will allow collection of several kinds of data, including home range dynamics, habitat use within home ranges, habitat selection at multiple levels (including that of small-scale habitat features), long-distance movements, and dispersal. Intensive telemetry studies also permit remote identification of individual animals, which, among other things, makes possible the attribution of behaviors observed while snow-tracking to a sex-age class. Obtaining some kinds of demographic data, including parturition rates and causes of mortality, also is facilitated with telemetry.

Intensive Demographic Studies

Intensive demographic studies are the most difficult of the study types discussed here, but these studies are essential to parameterize models of population persistence. Information from demographic studies includes longevity, parturition rates, sex-age structure, litter sizes, age- and sex-specific survivorship, ages and sex of dispersers, population growth rates, and mortality causes. Replication is important for these data categories in order to calculate variances for each of the attributes. Some types of data can be obtained from intensive live-trapping, others from telemetry. Demographic studies will be extremely labor-intensive with relatively small returns for energy and resources invested. The development of meaningful demographic data bases for forest carnivores is nonetheless essential, and a sustained commitment of resources to long-term intensive sampling will be necessary. For forest carnivores, demographic studies should be planned for no less than 10 years.

Extensive Studies of Species Occurrence

This type of study will be extensive in relation to landscape features. It addresses patterns of forest carnivore occurrence, and perhaps relative sighting frequencies, in relation to the major topographic, vegetative, land-use, and jurisdictional attributes of public forest lands of the western United States. Because surveys of the presence/ absence of forest carnivores often involve methods that conceivably can detect all four species, this type of study addresses information needs for multiple species, including forest carnivores not known to occur in an area. Several methods for detecting forest carnivores have been used in the past and are now being tested (Zielinski, pers. comm.). These techniques will require further evaluation before receiving wide application. Because of the extensive nature of this type of study, geographic information systems (GIS) would be needed. This type of study would benefit from currently-available spatially-explicit data bases and could be located to take advantage of them.

Ecosystem Studies

Ecosystem studies will support and provide a context for direct studies of forest carnivore populations and behaviors. Ecosystem studies will also help to elucidate the ecosystem processes that sustain forest carnivores, their prey, and forest vegetation. These studies include descriptions of vegetation patterns at landscape scales, which would be applicable to several forest carnivore species. The results of such studies will be analyzed and integrated with geographic information systems, and these studies would complement existing spatially explicit data bases. The ecology of prey, especially those that are important to more than one forest carnivore species, also would be investigated as a part of this effort. These studies would help to explain the variability in distribution and abundance of common prey of forest carnivores. It would also contribute to our understanding of how the prey of forest carnivores, including mice, squirrels, and hares, are affected by and contribute to ecosystem sustainability. These interactions include the relationships of these species to other important ecosystem components, such as lichens, mycorrhizal fungi, and conifer seeds. Ecosystem studies would also investigate community interactions among forest carnivores, and between forest carnivores and other vertebrate species that have similar resource needs. Such studies would provide insights into potential competitive and symbiotic interactions. In this context, ecosystem studies are essential for understanding the ecology of forest carnivores and for placing research results in an ecosystem management context.

Research Locations

Table 2 presents our specific research recommendations in terms of study types and locations. For purely practical reasons, we are not recommending that studies be replicated within ecoprovinces. However, we emphasize here that replication within ecoprovinces is important for optimal scientific credibility, and replications should be considered for some studies if resources permit.

We have recommended intensive telemetry-based and demographic studies in areas where species abundances make such studies possible and where information is needed. Our emphasis on the Northern Rocky Mountain Forest and Shining Mountains ecoprovinces reflects sympatric occurrence of up to all four forest carnivore species. In addition, our emphasis on these areas reflects urgent information needs associated with emerging concerns about the negative influences of forest management on forest carnivores in these areas. A similar situation exists for lynx in the Thompson-Okanogan Highlands ecoprovince and marten in the Colorado Rocky Mountains ecoprovince. Our recommendation that only extensive studies of occurrence be conducted in the Columbia Plateau ecoprovince is based on the relatively small amount of forested habitat within this area and on our assumption that forest carnivore distributions are limited here. We have recommended no intensive studies in areas where individual species' abundances appear to be too low for successful investigation.

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The marten, fisher, lynx, and wolverine are top predators in the ecosystems where they occur. As such, they influence and are influenced by all pertinent ecological processes. In addition, forest carnivores integrate landscapes via their large home ranges and high vagility, thus rendering them ideal subjects for research directed toward ecosystem management. The knowledge that is essential for ecosystem management is not attainable by studying "ecosystems" in some holistic fashion without also studying the component parts.

Ecosystem management will not be possible without detailed knowledge of individual species' ecologies. It is implicit in this statement that forest carnivore research must focus on the interactions between these predators and the ecological systems that support them. Most notably, we must develop a solid understanding of predator-prey relationships, interactions among sympatric predators, and the effects of landscape characteristics on ecological interactions. The landscape approach required for such studies will not be possible without spatially explicit ecological data and state-of-the-art GIS. We believe this kind of research is fundamental to successful ecosystem management.

Based on the preceding discussion, and considering the high level of research coordination and integration required, we recommend a programmatic approach to forest carnivore research. In addition to the advantages of programmatic leadership, we believe there are major logistical and scientific benefits to conducting research on more than one forest carnivore species in the same physical location. Indeed, this approach is essential for addressing certain questions. The fact of a common prey base and the need for sophisticated spatially explicit data bases makes the idea of a single study area even more compelling for some portion of the recommended research.

Table 2 reveals that all four forest carnivore species occur in the Northern Rocky Mountain Forest

Table 2.--Recommended locations and types of studies to be conducted within ecoprovinces. Numbers in cellis designate type(s) of recommended studies (1 = intensive, telemetery based; 2 = intensive, demography; 3 = extensive, patterns of occurence; 4 = ecosystem studies; X = species does not occur in abundances that would allow study; -- = no study recommended.)

Ecoprovince	Marten	Fisher	Lynx	Wolverine	Multi-species
Pacific Northwest Coast and Northern California Coast Ranges	1, 2	1, 2	X	X	3, 4
Columbia Plateau	--	--	--	--	3
Northern Rocky Mountain Forest	1, 2	1, 2	1, 2	1, 2	3, 4
Sierra Nevada	1, 2	1, 2	X	X	3, 4
Thompson-Okanogan Highlands	--	--	1, 2, 4	--	3
Shining Mountains	1, 2	1, 2	1, 2	1,2	3, 4
Utah Rocky Mountains and Colorado Rocky Mountains	1, 2, 4	X	X	--	3

and Shining Mountains ecoprovinces. Accordingly, we recommend the establishment of two study areas, one in each of these provinces, where all species and their prey base can be studied within an ecosystem framework. In this context, a single spatially explicit data base and the appropriate GIS technology would be developed for each set of studies. Given the geography involved, program leadership and a team of scientists responsible for research implementation should be established in western Montana. Existing Forest Service research facilities in Bozeman or Missoula would be ideal locations. Research in other ecoprovinces would be coordinated through this location, the Western Forest Carnivore Research Center. As part of its overall scientific leadership and coordination responsibility, this research center would be responsible for developing study plans, sampling protocols, and conducting pilot studies.

This overall approach could logically be expanded to other forest predators. All eight of the "sensitive" terrestrial vertebrates currently undergoing conservation assessments by the Forest Service are forest predators, including the four forest carnivores, the goshawk, and three species of forest owls. The grizzly bear, gray wolf, and mountain lion are sympatric with all eight in one of the ecoprovinces, the Shining Mountains, mentioned above. The avian predators are sympatric in both ecoprovinces mentioned, they share a common prey base with the smaller forest carnivores, and they will require a landscape approach for much of the needed research. Moreover, there are additional, potentially important, ecological relationships among the members of this complex predator community. Thus, from ecosystem management and scientific viewpoints, it would make sense to consider a research center chartered to study the ecology and behavior of all forest predators, in montane regions of the western United States. Indeed, such a center would in reality represent a center of excellence for ecosystem research where scientific efforts would be directed at the relationships among as many ecosystem dimensions as possible.

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Appendix A

Ecoprovinces of the Central North American Cordillera and Adjacent Plains[1]

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INTRODUCTION

The fundamental difference between the map presented here and other regional ecosystem classifications is that this map's ecological units are based on climatic processes rather than vegetation communities (map appears at the end of this appendix). Macroclimatic processes are the physical and thermodynamic interaction between climatic controls, or the relatively permanent atmospheric and geographical factors that govern the general nature of specific climates (Marsh 1988). This approach to regional ecological classification has proven useful to resource managers and interest groups in British Columbia (see British Columbia Commission on Resources and Environment 1994; British Columbia Ministry of Environment, Lands and Parks 1993; Hume 1993; Province of British Columbia 1993; Quesnel and Thiessen 1993; Senez 1994; Wareham 1991; Western Canada Wilderness Committee 1992).

The ecoregion mapping concepts from Demarchi (1993) and Demarchi et al. (1990) were applied to the map, but due to time and budgetary constraints existing ecoregion classifications had to be used. The resultant map uses ecoprovince lines and mapping concepts from the British Columbia Ecoregion map - 1:2,000,000 (Demarchi 1993); the Terrestrial Ecoregions of Canada - 1:7,500,000 (Ecological Stratification Working Group 1993); Regional and Zonal Ecosystems in the Shining Mountains - 1:500,000 (Demarchi and Lea 1992); Major Ecoregion Subdivisions of the Pacific Northwest - 1:2,000,000 (Demarchi 1991); and other mapping sources described below.

Canada. The ecoprovince units for Canada were adapted from the recent Terrestrial Ecozone and Ecoregion map of Canada (Ecological Stratification Working Group 1993). Ecoprovince units from Demarchi (1993) -1:2,000,000 had previously been incorporated into the Canadian Terrestrial Ecozones and Ecoregions map at 1:7,500,000. For Alberta, ecoprovince lines were adapted from Strong and Leggat's (1992) Ecoregions of Alberta - 1:1,000,000 map with additional consultation with Wayne Pettapiece (Agriculture Canada, Edmonton, Alberta) and Scott Smith (Agriculture Canada, Whitehorse, Yukon Territory). The Aspen-Parkland ecoprovince was adapted as a separate, transitional unit from either the Canadian Prairie or Boreal Lowland ecoprovinces from early work by Crowley (1967) and Bailey (1976). For Saskatchewan, the Ecoregions of Saskatchewan by Harris et al. (1983) were used to augment those of the Canadian map.

United States. For the United States portion of the map, ecoprovince lines were developed using the U.S. Department of Agriculture (USDA) Forest Service ECOMAP Team's map of Ecoregions and Subregions of the United States - 1:7,500,000 (see Bailey et al. 1993). It was used for broad ecoclimatic zona-

[1] *The ecological stratification scheme presented here shows spatial relationships of ecosystems in common to the United States and Canada. The relationships will be important in the development of conservation strategies for forest carnivores. The stratification scheme has much in common with the USDA Forest Service ECOMAP system (U.S, coverage only - Bailey et al. 7993) and is meant to be complementary to that system.*

tion concepts (ecodivisons) and a rough approximation of ecoprovinces. The U.S. Environmental Protection Agency's maps of Ecoregions of the Conterminous United States - 1:2,500,000 and 1:7,500,000 (Omernik 1986, 1987; Omernik and Gallant 1986, 1987a, 1987b, 1987c, 1989) were used for definition of physiographic units. Land Resource Regions and Major Land Resource Areas of the United States - 1:7,500,000 (USDA Soil Conservation Service 1978, 1981) was also used as a basis to aggregate or combine regional units into ecoprovinces. And the National Geographic Society's (1976) Landsat compilation was used for final physiographic definition. Mapping was conducted at 1:4,560,000, in order to be compatible with the composite Landsat image of the National Geographic Society (1976), which was the only available Landsat image for the entire project. Ideally, more detailed Landsat images at 1:250,000 should have been utilized. No attempt was made to correlate lines with vegetation community units (i.e., Brown and Lowe 1980; Franklin and Dyrness 1973; Idaho Department of Water Resources 1990; Kuchler 1975; Ross and Hunter 1976).

The U.S. Environmental Protection Agency map (Omernik 1986) often provided the best fit. But, there were many instances where instead of mapping regional ecosystems, that map approximated a zonation level. The map of ecoregion aggregations by Omernik and Gallant (1989) did not satisfy the identification of broad climatic classes.

The USDA Forest Service ECOMAP Team's map appeared to be at a broad level, perhaps at the scale of presentation (1:7,500,000) (see Bailey et al. 1993). There was a reliance on broad vegetation communities or patterns to reflect ecoclimate zones (Bailey, pers. comm., 1993).

The USDA Soil Conservation Service's (1978, 1981) Land Resource Areas map was based on soils, climate, and land use. Each Land Resource Region encompasses several climatic regions and major physiographic units and appears to be based more on current agricultural practices than on any ecological parameter or process. Land Resource Regions were broad groupings of the Land Resource Areas for agricultural planning purposes. The Land Resource Areas are quite detailed and approximate specific physiographic units or physical landscapes.

Mexico. The ecoprovince units that were defined for northern Mexico were developed from Brown and Lowe's (1980) Biotic Communities map, and Lowe and Brown's (1982) Biogeographic Provinces map.

ECODIVISION AND ECOPROVINCE DESCRIPTIONS

The following is a discussion of ecodivisions and ecoprovinces on the enclosed map, Central North American Cordillera and Adjacent Plains. The ecodivisions and ecoprovinces have not been put into an ecodomain framework because almost all of the mapped area falls within the Dry Ecodomain (see Bailey 1978). Ecoregions have also not been described as part of this current effort. Ecoregion information, however, is available for the Canadian portion (see Ecological Stratification Working Group 1993) and for the United States' portion (see Bailey et al. 1993; Omernik 1986; Omernik and Gallant 1986, 1987a, 1987b, 1987c). The author is unaware of any ecoregion descriptions for Mexico.

BOREAL PLAINS ECODIVISION (1)

This low-lying, upland and plains ecodivision lies at mid-latitudes across the Interior Plains from the Rocky Mountain Foothills in British Columbia and Alberta east to the Canadian Shield in Alberta, Saskatchewan, and Manitoba. The climate is continental, with cold Arctic winters and moderately warm summers. It contains two ecoprovinces.

Boreal Lowlands Ecoprovince

Landforms. This ecoprovince occurs predominantly on the Interior Plains, specifically the Alberta Plateau, northern Alberta Plain, northern Saskatchewan Plain and Manitoba Plain, which consist of low plateaus, plains, and lowlands. All were glaciated by the Laurentian Ice Sheet.

Climate. Cold, dry Arctic air masses are dominant in the winter and spring. In the summer and fall warmer, wetter Pacific westerlies dominate (Strong and Leggat 1992). Much of the summer and fall moisture is from surface heating of the many wetlands, streams, and lakes.

Vegetation. Quaking aspen with bluejoint, prickly rose, and bunchberry dominate most upland sites; wetter sites are dominated by quaking aspen and balsam poplar; poorly drained sites are vegetated by an overstory of black spruce with an understory of Labrador tea, bog cranberry, and mosses; jack pine communities are common on the uplands, but white spruce and black spruce are the potential climax forest species (Strong and Leggat 1992).

Boreal Uplands Ecoprovince

Landforms. This ecoprovince occurs on the Alberta Plateau and consists of plateaus, plains, prairies, and lowlands and is generally a rolling upland once away from the deeply incised river beds.

Glaciation. The entire area was glaciated during the Pleistocene by westward-moving ice sheets that originated in the Arctic of Hudson Bay and Baffin Island (Fulton 1989). A large glacial lake was formed in the Peace Lowland basin.

Climate. The climate is typically continental since most of the moist Pacific air has dried and crossed successive ranges of mountains before it reaches the area. Air movement is generally level, with intense orographic lifting in the vicinity of the Peace River. In warmer months, rain is largely caused by surface heating, which leads to convective showers. Winters are cold because there are no barriers to irruptions of Arctic air.

Vegetation. A single climax community, the boreal white and black spruce forest, dominates this ecoprovince. Quaking aspen seral forest occurs in the Peace River lowland and black spruce muskeg occurs throughout most of the upland surface. On the western-most areas, just east of the Rocky Mountain Foothills on low ridges, more mountainous vegetation develops such as the Engelmann spruce and subalpine fir forests that occur on the summits of those ridges.

HUMID CONTINENTAL HIGHLANDS ECODIVISION (2)

This complex mountains, plateaus, and basins ecodivision is situated at mid-latitudes across the central interior of British Columbia, from the Coast Mountains east to the Interior Plains and south into northeastern Washington, northern Idaho, and northwestern Montana. The climate is sub-continental with cold, commonly Arctic winters and warm, dry summers. Precipitation is predominantly from Pacific air masses, but surface heating of wetlands, streams, and lakes provides additional moisture. This ecodivisions contains three ecoprovinces.

Central British Columbia Plateaus Ecoprovince

Landforms. This ecoprovince consists of the flat to rolling Chilcotin and Cariboo plateaus and the southern two-thirds of the Nechako Plateau. It also contains the Chilcotin Ranges west to the center of the Pacific Ranges and the Bulkley and Tahtsa Ranges of the Kitimat Ranges. Those mountain ranges on the east side of the Coast Mountains are included because they are much drier than the windward side and therefore have a more interior-type of climate.

Glaciation. The entire area was glaciated during the Pleistocene, and ice sheets moved northeastward from the Coast Mountains. Glacial lakes and subsequent lacustrine deposits occur primarily in the Fraser River Basin area.

Climate. The area has an atypical continental climate: cold winters, warm summers, and a precipitation maximum in the late spring or early summer. However, the moderating influences of Pacific air occur throughout the year, as is the case for most of British Columbia south of 57N. This ecoprovince lies in a rain shadow leeward of the Coast Mountains. In summer there is intense surface heating and convective showers, and in the winter there are frequent outbreaks of Arctic air (these are less frequent than in the Sub-Boreal Interior ecoprovince to the north).

Vegetation. The area contains interior Douglas fir, pinegrass forests in the southern landscapes; lodgepole pine, quaking aspen, spruce forests in the center; and hybrid spruce, lodgepole pine and quaking aspen forests in the north. In addition, bunchgrass steppe with big sagebrush occurs within the deeply entrenched portions of the Fraser and Chilcotin rivers. Douglas fir, lodgepole pine, and pinegrass forests occur at middle elevations in the Chilcotin Ranges and southern Chilcotin Plateau. Engelmann spruce and subalpine fir forests occur on the middle slope of all mountains and the higher portion of the northern Chilcotin and southern Nechako Plateaus. Alpine occurs on all mountain summits.

Shining Mountains Ecoprovince

Landforms. This ecoprovince consists of six main physiographic systems: the highlands on the western flank, the Columbia Mountains, the Southern Rocky Mountain Trench, the Continental Ranges of the Canadian Rocky Mountains, the Rocky Mountain Foothills of Alberta (including the Porcupine Hills) and Montana, the Belt Formation or Border Ranges of the northern Rockies in Montana, and the mountains of the Panhandle of Idaho.

Glaciation. The entire area was glaciated during the Pleistocene, and the most intensive was the Cordilleran glaciation in the Columbia and Canadian

Rocky Mountains. Portions of the Rocky Mountain Foothills may have been unglaciated during periods of waning glaciation because this was the eastern boundary of the Cordilleran Ice Sheet and the western boundary of the Laurentian Ice Sheet. In the southern mountains, glaciers occurred on the upper slopes, but not in the valleys, even though glacial lakes often dominated those valleys.

Climate. Air masses approach from the west and lose moisture, first as they pass over the western Columbia Mountains and Bitterroot Ranges and. again as they pass over the Rocky Mountains. The Southern Rocky Mountain Trench bisects two large mountain blocks with similar physiography and macroclimatic processes. During the summer, intense surface heating creates strong updrafts in the mountains. The resulting downdraft over the center of the Rocky Mountain Trench clears the skies and enhances the sunny conditions. During the winter and early spring, outbreaks of Arctic air bring cold, dense air to the Rocky Mountain Foothills and eastern Rockies. The Rocky Mountain Trench serves as an access route for Arctic air that occurs in the Sub-Boreal Interior of ecoprovince.

Vegetation. Four climax communities dominate this ecoprovince: the interior western redcedar and western hemlock forests in the lower to middle slopes of the Columbia Mountains and Bitterroot Ranges and wetter localities in the Rockies and northern portion of the Rocky Mountain Trench; the interior Douglas fir, bunchgrass, bitterbrush forests of the Southern Rocky Mountain Trench lower slopes of the Clark Fork Valley; Engelmann spruce and subalpine fir forests on the middle slopes of all mountains; and dry, rock dominated alpine tundra on the mountain summits. In addition, ponderosa pine, bunchgrass, and bitterbrush forests occur in the Southern Rocky Mountain Trench. Douglas fir, lodgepole pine, and pinegrass forest occurs in the valleys and lower slopes of the Continental and Border ranges of the Rockies and eastern Purcell Mountains; the interior Douglas fir and grand fir forests occur sporadically c)n mid slopes in the Coeur d'Alene Mountains and in the Clark Fork Valley. Quaking aspen parkland with rough fescue occur at lower slopes in the Rocky Mountain Foothills.

Sub-Boreal Interior Ecoprovince

Landforms. This ecoprovince consists of several physiographic systems: the Coast Mountains, the Interior Plateau, the Omineca Mountains and the Rocky Mountains. The mountains in the west include the southeastern portion of the Boundary Ranges and the Skeena Mountains. The mountains to the north include the southern Omineca Mountains. The mountains to the east include the Misinchinka and Hart ranges of the Rocky Mountains and associated Foothills. In the center and south is the low-lying plateau area of the Nechako Lowlands and northern portion of the Nechako Plateau.

Glaciation. The entire area was glaciated during the Pleistocene by glaciers that coalesced on the plateaus and lowlands. Glaciers moved southeast from the Boundary Ranges and south from the Skeena and Omineca Mountains. They met glaciers that moved northeastward across the Interior Plateau and moved together over the Hart Ranges (Claque 1989). Large glacial lakes formed in the Nechako Lowland and Northern Rocky Mountain Trench.

Climate. Prevailing westerly winds bring Pacific air to the area over the Coast Mountains by way of the low Kitimat Ranges or the higher Boundary Ranges. Much of this area is in a rain shadow. Coastal air has low moisture content when it arrives. Moisture does enter the area when there is a southwest flow over the low Kitimat Ranges. Summer surface heating leads to convective showers, and winter frontal systems result in precipitation that is evenly distributed throughout the year. Outbreaks of Arctic air are frequent. The southern boundary of the Ecoprovince approximates the southern boundary of the Arctic air mass in January.

Vegetation. Sub-Boreal spruce forests with hybrid spruce, subalpine fir, and lodgepole pine dominate the Nechako Plateau, Nechako Lowlands, Northern Rocky Mountain Trench, and many of the valleys. Engelmann spruce and subalpine fir forests occur on the middle slopes of all mountains, and alpine tundra occurs on the upper slopes of those mountains. In the wetter valleys of the Skeena Mountains, interior western redcedar and western hemlock forests occur. In the northern Omineca Mountains and valleys of the Rocky Mountain Foothills, forests of white spruce, lodgepole pine, quaking aspen, and black spruce occur.

HUMID CONTINENTAL PLAINS ECODIVISION (3)

This plains ecodivision is situated at mid-latitudes across the Interior Plains of Alberta, Saskatchewan,

and Manitoba, and then south on the Red River Plain of North Dakota and Minnesota. This area is transitional between the boreal, continental climate to the north and the prairie continental climate to the south and west. Winter consists of cold, dry, Arctic air, while summers are hot and humid with surface heating of wetlands, streams, and lakes. There are two ecoprovinces but only one for this project.

Aspen-Parkland Ecoprovince

Landforms. This ecoprovince occurs on gently undulating to rolling glacial deposits, usually consisting of packed morainal, coarse flood-washed, or finer lake-deposited materials (Klassen 1989).

Climate. The winter climate is affected by a ridge of high pressure that usually extends from the Gulf of Alaska to Hudson Bay. The cold, dense Arctic air from the north generally deflects the milder, westerly Pacific air southward. Winters are long and severe. Summer and spring climates are warm and humid, often being affected by moist air from the Gulf of Mexico (Hare and Thomas 1979).

Vegetation. Quaking aspen that occur as clones are surrounded by rough fescue, bluebunch fescue, junegrass, and needlegrasses that dominate the natural landscape. Quaking aspen and balsam poplar stands occur on moister sites. Eastern cottonwood, green ash, and Manitoba maple are common along the riparian areas. In the eastern portion, quaking aspen and bur oak communities dominate (Harris et al. 1983; Strong and Leggat 1992). The natural ecosystems of the entire area have been affected by the reduction of wildfire, the elimination of free-ranging plains bison, and cultivation (Harris et al. 1983).

HUMID MARITIME AND HIGHLANDS ECODIVISION (4)

This ecodivision consists of complex coastal marine areas, lowlands, archipelagos and rugged mountains. It lies perpendicular to the prevailing Northeast Pacific air masses and the Sub-Arctic Current of the Northern Pacific Ocean. The climate is generally wet and mild throughout the year, with hot, dry periods in the late summer in the south, and with intense precipitation during the fall, winter, and early spring. Arctic air invades this area only infrequently. There are two ecoprovinces.

Georgia-Puget Basin Ecoprovince

Landforms. This ecoprovince is a large basin that encompasses the southeastern Vancouver Island Mountains, the Nanaimo Lowlands, the Strait of Juan de Fuca and the eastern slopes of the Olympic Mountains in the west; the Strait of Georgia, Gulf Islands, and Puget Sound in the middle; and the Georgia Lowlands, Fraser Lowlands, Puget Lowlands in the east.

Climate. Pacific air reaches this area primarily after lifting over the Insular and Olympic mountains. That air descends into the central straits and sounds before it rises over the extensive Pacific and Cascade ranges. Surface air flow is level or subsiding and creates clearer and drier conditions than in coastal areas adjacent to the Pacific Ocean. Temperatures throughout the area are modified by the ocean and marine environments and only exceptionally will Arctic air flow over the Pacific Ranges to bring short periods of intense cold and high winds.

Vegetation. Temperate rainforests dominated by western hemlock, Douglas fir, and western redcedar occur on most mountain and upland sites. Low elevation plains and rocky sites along the western portion are dominated by coastal Douglas fir and salal forests. Garry oak and arbutus trees occur northward along eastern Vancouver Island and the Gulf Island, giving the coastline of this area a Mediterranean appearance. Mountain hemlock and subalpine forests occur on the higher portions of the Vancouver Island Ranges.

Pacific Northwest Coast and Mountains Ecoprovince

Landforms. This ecoprovince includes the windward side of the Coast Mountains, Coast Range, Cascade Range, Vancouver Island, all of Queen Charlotte Islands, the Alexander Archipelago, St. Elias Mountains, and the continental shelf from Cook Inlet to southern Oregon. Large coastal mountains, a broad coastal trough and the associated lowlands, islands, and continental shelf also occur here.

Glaciation. This ecoprovince was glaciated most heavily in the northern portion and less so in the Cascade Range but was unglaciated in the Coast Range and Willamette Valley of Washington and Oregon. Glaciers and ice-sheets that originated along the crest of the coast mountains moved west and southward to the ocean, sculpting the valleys and faults into fjords and channels. Even the continental

shelf was affected as it received the glacial debris and outwash, forming a deep blanket of sediment.

Climate. The major climatic processes involve the arrival of frontal systems from the Pacific Ocean and the subsequent lifting of those systems over the coastal mountains. In winter, oceanic low pressure systems dominate the area and pump moist, mild air onto the entire coast. In the summer, high pressure systems occur over the north Pacific Ocean and low pressure frontal systems become less frequent in the southern portion and tend to strike the coast of Alaska.

Vegetation. Temperate rainforests of western hemlock, yellow cedar, western redcedar, and sitka spruce dominate most of the mountains and lowlands. Mountain hemlock subalpine forests and alpine tundra communities occur on the mountain summits. Glaciers are common, and large icefields persist on the St. Elias Mountains, Boundary, and Pacific ranges. More locally, drier coastal Douglas-fir forest occurs in the Willamette Valley; interior western redcedar and western hemlock forests occur in the Nass Basin, a coast-interior transition area; and Engelmann spruce, subalpine fir, and boreal white spruce and black spruce forests occur along eastern-most valleys that lead into the interior of the continent.

MEDITERRANEAN HIGHLANDS ECODIVISION (5)

This coast, foothills, basins, and mountains ecodivision occurs at south to mid-latitudes from Baja California north across California to southern Oregon. This area lies perpendicular to the West Wind Drift and California Current of the Northern Pacific Ocean and to Pacific air masses. This wet, mild air mixes with the hot, dry, desert air of the interior creating a strong Mediterranean climate-a wet winter followed by a dry summer. In this current effort, four ecoprovinces have been recognized, but further evaluation is required to determine if such a designation is warranted.

California Coast and Foothills Ecoprovince

Landforms. This ecoprovince includes the Central Western and Southwestern California Geographic subdivisions (Hickman 1993), which extend south onto the Baja California peninsula to approximately 30ºN (Brown and Lowe 1980; Lowe and Brown 1982). The South Coast and Peninsula ranges are a series of northwest-southeast trending foothills and valleys, whereas the Transverse Ranges are oriented east-west. This ecoprovince also includes the coast and islands such as the Channel and Farallon islands and the continental shelf from Bahia Santa Marie north to San Francisco Bay.

Climate. Prevailing westerly winds dominate this area. Moderate temperatures and moisture meet hot, dry interior climates, creating fog that persists along the coast and windward side of the mountains. Seasons are dominated by wet, cool months in the winter and early spring, and by dry, hot months from late spring to fall (Munz and Keck 1970).

Vegetation. Forests include thick-leaved species of California live oak, canyon live oak, interior live oak, California laurel, arbutus, and Pacific bayberry on the north-facing slopes; chapparal shrubland of chamiso, manzanita, Christmasberry, California scrub oak, and mountain mahogany on the south-facing and drier sites; and sagebrush-steppe of soft chess, cheatgrass, and California sagebrush on the coastal plains and interior valleys.

Great Central Valley Ecoprovince

Landforms. This ecoprovince is a low elevation, broad alluvial valley bordered by sloping fans, dissected terraces, and low foothills (Bailey 1978; Munz and Keck 1970).

Climate. Moist Pacific air rises over the Coast Ranges to the west creating a rainshadow in the Great Central Valley. The prevailing winds from the west also help to moderate the hot, dry air from the deserts to the southeast. An important climatic factor is the fog that occurs in the winter, bringing humid, cool conditions to this area (Munz and Keck 1970).

Vegetation. This ecoprovince has been converted to agricultural and urban developments, but the potential dominant vegetation is needlegrasses and threeawns. At present, the undeveloped areas are dominated by annual grasses such as bromes, fescues, and oats. Chapparal or broad-leaved sclerophyllic shrub vegetation occurs in sporadic patches as do southern oak woodlands (Munz and Keck 1970). The rivers flow through alkaline flats where greasewood, picklewood, saltgrasses, and shad scale are prevalent. Tule marshes border the lower reaches of the San Joaquin and Sacramento rivers (Bailey 1978).

Sierra Nevada Ecoprovince

Landforms. This ecoprovince is composed of the southern portion of the Cascade Ranges and the high, rugged Sierra Nevada. Some mountains had glaciers during the Pleistocene epoch. The Sierra Nevada consists of an immense granitic batholith. While its steep eastern face rises abruptly above the Great Basin to the east, the western slope is a more gradual tilted plateau that is scored with deep canyons (Hickman 1993; Munz and Keck 1970).

Vegetation. On the western foothills dense stands of blue oak and Digger pine occur with scrub live oak. Annual grasses such as chess, wild oats, and ripgut brome are dominant understory species. Vegetation changes from ponderosa pine, manzanita, and black oak, to forests of Douglas fir, incense cedar, sugar pine, lodgepole pine, and then to red fir, Jeffery pine, mountain hemlock, and white-bark pine forests with rising elevation. Bristlecone pine grows at treeline. Alpine occurs on the highest summits. Giant Sequoia grow in the moist southern valleys (USDA Soil Conservation Service 1981).

Northern California Coast Ranges Ecoprovince

Landforms. This ecoprovince is composed of the Klamath Mountains and Coast Ranges of northern California and extreme southwestern Oregon. The province rises in a series of low hills and mountains from the Pacific Coast.

Climate. The climate is greatly influenced by the Pacific maritime westerlies that baring mild temperatures and intense moisture during the winter and spring. During the summer and fall, hot, sub-tropical desert air arrives from the east and south.

Vegetation. Forests range from western hemlock, grand fir, Sitka spruce to Douglas fir, arbutus, broadleafed maple. Wet, fog-dependent redwood forests with Douglas fir, salal, and rhododendron occur along the coast (Hickman 1993; Munz and Keck 1970).

SEMI-ARID STEPPE HIGHLANDS ECODIVISON (6)

This basin, plateau, and mountain ecodivision lies east of the Coast Mountains and Cascade Ranges of southern British Columbia, Washington, and northern Oregon. Much of the western area is in the rainshadow of those mountains. Pacific air is generally level and sub-continental in effect and does not contribute much precipitation, until it reaches the mountains to the east. Winters are cold and dry and usually not affected by cold, Arctic air; summers are warm to hot and dry, but with peak precipitation in the early growing season. Three ecoprovinces are recognized in this current effort, but the complex Northern Rocky Mountain Forest ecoprovince should be re-evaluated.

Columbia Plateau Ecoprovince

Landforms. This Ecoprovince is predominantly a level surface of Tertiary lavas that have been deeply dissected by the Columbia and Snake rivers. Much of the northeastern portion has been scoured by excessive flooding during the later stages of the Pleistocene glaciation (Alt and Hyndman 1984; Thornbury 1969). This ecoprovince also includes the dry-forested, leeward portion of the Cascade Ranges.

Climate. The climate of this area is moderated by the surrounding mountains. Much of the moisture has been precipitated from the westerly Pacific air masses as they cross the Cascade Ranges. The air flowing down the leeward slopes warms and retains moisture as it crosses the plateau. The great chain of mountains to the north and east protect this area from all but severe outbreaks of Arctic air in the winter and spring. In the late summer and early fall, hot sub-tropical air can move in from the south prolonging the hot, dry summer conditions (Franklin and Dyrness 1973).

Vegetation. Dominant vegetation typically includes big sagebrush, pasture sage, bluebunch wheatgrass, and bluebunch fescue, rough fescue, and snowberry occur with increased elevation to the east. In the mountains, ponderosa pine forests give way to Douglas fir and grand fir montane forests, which give way to subalpine forests of Engelmann spruce, grand fir, subalpine fir, and lodgepole pine on the upper forest slopes and higher valleys. Alpine tundra communities occur on the summits of the higher mountains (Daubenmire 1970; Franklin and Dyrness 1973).

Northern Rocky Mountain Forest Ecoprovince

Landforms. This ecoprovince consists of several mountain ranges with different origins that collectively form a major east-west mountain block. The Blue Mountains in the west are predominantly of

sedimentary and volcanic origins, with wide, raised valleys and deep dissected river gorges. The mountains of central Idaho consist of the Idaho Batholith and are high and rugged, with deep narrow valleys. The mountains of eastern Idaho and Montana are Precambrian volcanic and sedimentary with high rugged ridges rising abruptly from wide flat-bottomed valleys. The mountains of Wyoming are volcanic, with high valleys and higher mountain ranges (McKee 1972).

Glaciation. These mountains were not overridden by glacial ice-sheets but were sculpted by mountain glaciers in the Clearwater Mountains of Idaho, the Bitterroot Ranges, and mountain ranges in Wyoming.

Climate. The mountainous topography of this ecoprovince results in a very complex climate. It receives the Pacific westerlies after they have crossed the Cascade Ranges and the Columbia Plateau, giving added moisture to the western flank. These mountains are also a barrier to outbreaks of Arctic air flowing southwestward across the Interior Plains of North America or southward across the interior of British Columbia. In the summer and fall this ecoprovince receives intense heat from southern subtropical air masses.

Vegetation. The plant communities are complex in lower elevations and includes big sagebrush, bluebunch wheatgrass stands. Douglas fir, grand fir, and ponderosa pine forests dominate the middle elevations; Engelmann spruce, lodgepole pine, and subalpine fir occur on the upper mountain slopes; and alpine communities occur only on the highest mountains in the eastern portion of this area (Bailey 1978; Ross and Hunter 1976; Steele et al. 1983).

Thompson-Okanogan Highlands Ecoprovince

Landforms. This ecoprovince includes the Thompson Plateau, the Pavilion Ranges, the eastern portion of the Cascade Ranges south to Lake Chelan, the western margin of the Shuswap Highlands, and the Okanogan (spelled Okanagan in Canada) Highlands. The leeward portion of the coastal mountains and the drier portion of the highlands are included because they share much the same climate as the main plateau area.

Climate. Air moving into this ecoprovince from the Pacific has already lost most of its moisture on the west-facing slopes of the coastal mountains. The air moving across the plateau surface tends to be level, resulting in little precipitation, except through surface heating of lakes and streams. There are occasional irruptions of hot, dry air from the Great Basin to the south in the summer. They bring clear skies and very warm temperatures. In winter and early spring, frequent outbreaks of cold, dense Arctic air occur because there is no effective barrier once it enters the interior plateaus of British Columbia. However, such events are less frequent than on the plateaus farther north.

Glaciation. Pleistocene glaciation was very intense throughout, except for the portion in Washington where valley glaciers and mountain glaciers remained distinct. Large glacial lakes formed and then were filled with silt in the Thompson, Nicola, and Okanagan valleys.

Vegetation. Three climax plant communities dominate this ecoprovince: the bunchgrass steppe, often with big sagebrush in the lower slopes of the large basins; the interior Douglas fir and bunchgrass forests on the lower elevations of the plateau surface; and the Douglas fir, lodgepole pine and pinegrass forests on the higher elevations of the plateaus and highlands. Engelmann spruce, subalpine fir forests occur on the higher elevations of the plateau and on the middle to upper slopes of the mountain ranges. On the highest summits of the Okanagan and Pavilion ranges, alpine tundra occurs. Ponderosa pine, bunchgrass, and rabbitbrush parkland occur sporadically on the middle slopes of the large, dry basins.

SUB-TROPICAL DESERTS ECODIVISION (7)

This complex coastal, basin, plateau, and mountain ecodivision lies at mid-southerly latitudes in northern Mexico and the southwestern United States. Climate is extremely arid with high temperatures. Days are very hot, but nights are cold due to outgoing radiation causing extreme day to night temperature variation. Three ecoprovinces have been delineated for this project, but more are likely to occur in Mexico.

Chihuahuan Desert Ecoprovince

Landforms. Broad desert basins and valleys are bordered by gently sloping to strongly sloping fans and terraces. Steep north-south trending mountain ranges and many small mesas occur in the west (USDA Soil Conservation Service 1981).

Climate. Most of the precipitation comes in convectional storms during the summer months; rain and even snow in the mountains fall occasionally in the winter. The most arid season is late spring and early summer. Due to the high elevation, mean temperatures are moderate but the summer days are hot (Bailey 1978; USDA Soil Conservation Service 1981).

Vegetation. In the eastern plains and basin, vegetation consists of Trans-Pecos shrub savanna on the lower plains, changing to grama-tobosa prairie and finally to oak-juniper woodland with rising elevation. In the western mountains and mesas, grama-tobosa shrubsteppe occurs at the lower elevations changing to oak-juniper woodland and finally to Arizona pine forest on the summits of the highest mountains (Brown 1982d, 1982e).

Sonoran-Mojavian Deserts Ecoprovince

Landforms. This ecoprovince is characterized by extensive, undulating plains from which isolated low mountains and buttes abruptly rise. The mountains are rocky but flanked by alluvial fans and outwash aprons. Most minor rivers are dry most of the year (Bailey 1978).

Climate. The climate is characterized by long, hot summers, though the winters are moderate and frosts are common. In the winter, the rain is gentle and widespread but in summer thunderstorms are prevalent. In some years, in the western portion, there may be no measurable precipitation (Bailey 1978).

Vegetation. Plant cover is usually very sparse, with bare ground between individual plants. Cacti and thorny shrubs are conspicuous, but many thornless shrubs are also present. Creosote bush is widespread on the Sonoran Desert Plains. Aborescent cacti and cholla are also common. Mesquite grows along washes and watercourses. On steep rocky slopes paloverde, ocotillo, saguaro, cholla, and compass barrel cactus are abundant. Along the higher, northern portion is a belt of junipers and pinyons (Bailey 1978; Turner and Brown 1982).

Sierra Madre Occidental Ecoprovince

Landforms. This ecoprovince consists of mature, rolling volcanic plateaus, cumulating in high mountains. Deep, rugged canyons dissect the plateaus and mountains (Gordon 1968).

Climate. In general the climate is dry, although there are light winter and heavy summer rainy seasons; early spring is very dry. This pattern falls between the summer-rain type in central and southern Mexico and the winter-rain type of California. The winters are characterized by low relative humidities and are cold with many hard frosts. At higher elevations light snowfalls are common (Gordon 1968).

Vegetation. The vegetation is a complex of Mexican oak-pine forests. Ponderosa pine is common but there are a dozen other species as well, such as scrub oak, Arizona cypress, true fir, Douglas fir, prickly pear, barrel cactus, and accacia. A dense, low, chapparal-like woodland dominated by scrub oak and acacia grows above the oak-pine forests. In the foothills, a large variety of oaks occur in both the live oak (encinal) and oak-pine woodlands (Brown 1982b; Meyer 1973; Pase and Brown 1982).

SUB-TROPICAL SEMI-DESERT HIGHLANDS ECODIVISION (8)

This complex basin, plateau, and mountain ecodivsion lies in northern Arizona, New Mexico, southern Utah, and southwestern Colorado. The climate is transitional between that of the extreme deserts to the south and the more temperate climates to the north. The hot, dry climates are moderated by the elevation of the plateaus and mountains. There are three ecoprovinces.

Arizona Mountains Ecoprovince

Landforms. This ecoprovince is a series of mountains, ridges, and mesas, culminating on the Mogollon Rim. The area is very hilly and mountainous, but the upland plateau is dissected by many deep canyons (USDA Soil Conservation Service 1981).

Climate. The area is affected by hot, moisture-laden air arriving from the Pacific Ocean to the west and occasionally from the Gulf of Mexico to the southeast. Such air is heated as it crosses over the American deserts. Half of all the precipitation that falls here occurs during the growing season (Pase and Brown 1982).

Vegetation. Climax plant communities occur as successive belts that change with elevation and protection from desert air. On the southwestern side, sagebrush-steppe gives way to oak-juniper scrub, which changes to ponderosa pine forests. At the highest summits, notably the San Francisco, White, Mogollon, Black, Mateao, and Magdelena mountains, spruce-fir/Douglas-fir forests are established. Alpine

tundra occurs on only the tallest of those summits (Humphrey Peak). On the east or Colorado Plateau side, pinyon-juniper woodland is established (Brown 1982a; Pase and Brown 1982).

Colorado Plateaus Ecoprovince

Landforms. This ecoprovince is surrounded by mountains: to the south are the Arizona Mountains, to the east are the Rocky Mountains of Colorado and New Mexico, and to the northwest are the Rocky Mountains of Utah. The northern portion of the Colorado Plateau physiographic unit is affected by more temperate climates and is therefore considered to be another ecoprovince (the Central Rocky Mountain Basins ecoprovince). The Colorado Plateaus ecoprovince consists of the Grand Canyon, Kaibab Plateau, Painted Desert, and San Juan River Valley mesas and plateaus. In general the surface consists of gentle to strongly sloping plains. Volcanic plugs rise abruptly from those plains and deeply incised canyons interrupt the plains' surface (USDA Soil Conservation Service 1981).

Climate. The climate is characterized by high altitude and cold winters. Summer days are usually hot, but nights are cool. Accordingly, diurnal temperature variation is considerable. Summer rains are thunderstorms, but ordinary rains and snowfall come in winter (Bailey 1978, USDA Soil Conservation Service 1981).

Vegetation. The plateau surface consists of Great Basin sagebrush, pinyon-juniper woodland, and grama-galleta steppe. Within the Grand Canyon, creosote bush, saltbush-greasewood, and blackbrush occur (Turner 1982).

New Mexico Rocky Mountains Ecoprovince

Landforms. This ecoprovince is dominated by high, rolling plateaus, with isolated mountains and steeply scarped mesas (USDA Soil Conservation Service 1981).

Climate. The climate is characterized by cold, high elevation winter temperatures and hot summers, although evening temperatures are cool due to rapid high-elevation heat loss. Precipitation usually occurs in winter as rain or snow; thundershowers are typical of summer precipitation (Bailey 1978).

Vegetation. Grassland vegetation of Indian ricegrass, blue grama, dropseed, prickly pear, four-winged saltbush, winterfat, and rabbitbrush gives way to pinyon-juniper woodlands, with big sagebrush at higher elevations. Douglas fir and ponderosa pine grow in more sheltered locations or at higher elevations. On the highest summits, Engelmann spruce and subalpine fir forests occur (Brown 1982b, Pase and Brown 1982).

TEMPERATE SEMI-DESERTS ECODIVISION (9)

This ecodivision is a broad expanse of basins and intervening mountain ridges situated in Nevada, western Utah, southern Idaho, southeastern Oregon, and northeastern California. It has a predominantly semi-arid continental climate with periodic summer rainfall but high temperatures. Winters are cold and dry, and summers warm to hot. This area contains two ecoprovinces.

Great Basin Ecoprovince

Landforms. This ecoprovince consists of the extensive isolated ridges and mountains and wide inter-valleys called the Basin and Range Province (Omernik 1986). The highest accumulation of mountains occur in central Nevada. Most streams do not drain to the sea.

Climate. Summers are hot and dry, and precipitation occurs in the cool winter months.

Vegetation. The landscapes are dominated by much-branched, non-sprouting, aromatic, semi-shrubs with evergreen leaves, such as sagebrush, shadscale, blackbrush, winterfat, greasewood, or rabbitbrush. There are few cacti, and those present tend to be of short stature or prostrate and include chollas, prickly pears, and hedgehog cacti (Turner 1982).

Snake River Basins Ecoprovince

Landforms. This ecoprovince consists of the broad Snake River Plain, Owyhee Mountains, Harney Basin, High Lava Plain, and Black Rock Desert. It also includes the Fremont Mountains of Oregon. Topography is dominated by level Tertiary basalts with deep dissected rivers or stretched landscapes of Basin and Range formations (McKee 1972).

Climate. The climate is influenced by the high mountains to the west, which create a rainshadow for westerly Pacific air masses. The Northern Rocky Mountain Forest ecoprovince also provides an effective barrier to Arctic air moving southwestward

across the Interior Plains or southward through the interior of British Columbia. Summers are hot and dry; precipitation is evenly distributed in fall, winter, and summer (USDA Soil Conservation Service 1981).

Vegetation. Climax plant communities are dominated by sagebrush with wheatgrass; saltbush and greasewood occur on alkaline soils. The northern occurrence of desert communities occur within Harney Basin. Western juniper with ponderosa pine and Douglas fir occur on the higher uplands (Bailey 1978).

TEMPERATE SEMI-DESERT HIGHLANDS ECODIVISION (10)

This is a complex basin, plateau, and mountain ecodivision, situated in eastern Utah, central Wyoming, western Colorado, and north-central New Mexico. It has a semi-arid continental climate that is strongly influenced by the generally high elevations of its plateaus and mountains. Winters are cold and dry, with Arctic air frequently lying along the eastern mountains. Summers are warm to hot with considerable precipitation. This area has four ecoprovinces.

Central Rocky Mountain Basins Ecoprovince

Landforms. This ecoprovince consists of many basins, such as the Green River, Uinta and Paradox, and many mountain ranges such as the Roan, Uncompahgre, White River, northern Colorado Plateaus, and Grand Mesa (Mitchell 1993).

Climate. The climate of this ecoprovince is moderated by the surrounding mountains, with complex rising and descending air masses. Maximum precipitation occurs in the winter and spring as Pacific air masses are deflected south around the Arctic air lying in the Interior Plains of North America. In the summer, sub-tropical air masses bring hot, dry weather, although the high elevation of this area causes most of the day-time air to dissipate at night.

Vegetation. This area supports sagebrush-steppe of big sagebrush, needle-and-thread bluebunch wheatgrass, and western wheatgrass. At higher elevations, big sagebrush, rabbitbrush, and winterfat form dense shrub communities with needlegrasses, Arizona fescue, and bluegrasses. Rocky Mountain juniper occurs on shallow upland soils. Ponderosa pine, Douglas fir, and quaking aspen forests occur on low mountain ridges (USDA Soil Conservation Service 1981).

Colorado Rocky Mountains Ecoprovince

Landforms. This ecoprovince consists of very high mountains with wide, high elevation valleys often called "parks." Mountain glaciers during the Pleistocene sculpted most of the mountain summits.

Climate. In the winter moist Pacific westerlies move across Oregon and Idaho and then deflect south of Arctic air masses lying over the Great Plains. The contact of the moist and cold air masses bring frequent snow storms to this ecoprovince. Arctic air can also flow over this area during periods of intense outbreaks. In the summer the intense heat of the subtropical air masses is ameliorated by the nocturnal dissipation of surface heat, due to the high elevations.

Vegetation. Climax plant communities are divided into elevational belts; sagebrush-steppe of big sagebrush, rabbitbrush, needlegrasses, and wheatgrasses give way to ponderosa pine and Douglas fir with junegrass and Arizona fescue. Quaking aspen communities occupy mid-elevations sites along with lodgepole pine and Engelrnann spruce forests. Grasslands and mountain meadows can be found within all mountains. On the summits, rolling alpine tundra or bare rock is common (Mitchell 1993).

Utah Rocky Mountains Ecoprovince

Landforms. This ecoprovince consists of two dominant mountain ranges, the Uinta and Wasatch Mountains, and a series of smaller ranges to the south.

Climate. The climate is affected by Pacific westerlies, which bring considerable winter and spring precipitation, in spite of the Great Basin Desert to the west. Precipitation is equal in summer and winter, with snow being common in the winter. Cold Arctic air often invades this area, having no effective barrier to the east. Summers are warm, but thunderstorms and convective showers bring periodic precipitation. Mountains in this area cool off rapidly in the evening due to their elevation.

Vegetation. Climax plant communities are variable with grassland steppe, mountain shrub, quaking aspen, conifer forests, and alpine rising in sequence with elevation. Big sagebrush and bluebunch wheatgrass are common sagebrush-steppe species. Quaking aspen forests are dominant over much of the landscape (Mueggler and Campbell 1986). Conifer for-

ests at higher elevations consist of Douglas fir, ponderosa pine, Engelmann spruce, white fir, subalpine fir, and lodgepole pine. Curlleaf and birchleaf mountain mahogany, Gambel oak, serviceberry, and chokecherry shrub communities are also abundant. Alpine tundra communities occur on the highest mountain summits (Mauk and Henderson 1984; USDA Soil Conservation Service 1981).

Wyoming Basins Ecoprovince

Landforms. This ecoprovince is composed of a series of high-elevation basins and low ridges; it also includes the Rocky Mountain outlier-the Bighorn Mountain range.

Climate. Summers are short and hot, the high elevation causes great diurnal temperature fluctuations, and the winters are cold. Arctic air can invade this area unimpeded from the northeast, while Pacific westerlies bring moisture. When the two systems coalesce, snow usually results.

Vegetation. Sagebrush-steppe, usually big sagebrush, bluebunch wheatgrass, shad scale, blue grama, needlegrasses, or fourwing saltbush are dominant in the wide basins. Pinyon pine, juniper, ponderosa pine, and Douglas fir forests occur with rising elevations, giving way to Engelmann spruce and lodgepole pine on the higher elevations (Green and Conner 1989; USDA Soil Conservation Service 1981).

TEMPERATE STEPPE PLAINS ECODIVISION (11)

This expansive plain ecodivision extends across the Interior Plains of southern Alberta and Saskatchewan, eastern Montana, Wyoming, Colorado, and western North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma. It has a strong semi-arid continental climate. Cold, usually Arctic winters in the northern portion and warm to hot summers with considerable precipitation occur. The high elevation of the southern portion effectively cools the area so that both northern and southern portions are similar. This area has three ecoprovinces, two of which are shown on the map.

Canadian Prairie Ecoprovince

Landforms. This ecoprovince occurs on the southern portions of the Alberta Plain and Saskatchewan Plain and includes elevated features such as the Cypress Hills, Sweetgrass Hills, and Bearpaw Mountains. It is generally a rolling upland with packed glacial till, coarse glacial-river deposits, and fine glacial lake sediments overlaying level Cretaceous, shale, siltstone, and sandstone. The large rivers are dissected below the upland surface (Beaty 1975; Klassen 1989).

Climate. The climate is continental, with bitterly cold winters and short but warm summers, with a light precipitation regime. In the west the Cordillera modifies the eastward-flowing Pacific air, causing warmer and drier conditions to prevail. In the east sub-tropical air from the Gulf of Mexico causes increased humidity and precipitation (Hare and Thomas 1979).

Vegetation. Needlegrasses, blue grama, and pasture sage dominate the southern and eastern portions. Rough fescue, Parry oatgrass, junegrass, lupines, and northern bed-straw dominate on the higher uplands to the west and near the Aspen-Parkland ecoprovince. At higher elevations on the upland outliers are quaking aspen, lodgepole pine, needlegrasses, wheatgrasses, lupines, and fescues; Douglas fir and ponderosa pine occur on the Sweetgrass Hills and Bearpaw Mountains (Ross and Hunter 1976).

Northern Great Plains Ecoprovince

Landforms. This ecoprovince is a high elevation plain, often called the High Plains or Rocky Mountain Pedimount. It is a rolling upland, often with a steep mountain outcrop that is more typical of the Rocky Mountain Foothills than of the surrounding plains. Being unglaciated, these plains have had a long period of erosion, resulting in wide valleys set between hard rock ridges. In some cases the streams are deeply incised.

Climate. Winters are cold and dry, and summers are warm to hot. Summer precipitation is a result of surface heating of streams. Arctic air may penetrate a considerable way southward, but the winter climate is as much a result of elevation as it is of Arctic air masses.

Vegetation. Native plant communities are typical of the shortgrass prairie: buffalograss, bluegrama, bluebunch wheatgrass, western wheatgrass, needle-and-thread, western needlegrass, and big sagebrush are common plains species. Much of the original vegetation has been replaced with cereal crops and occasionally with irrigated crops. In the mountain outcroppings, ponderosa pine, spruce, and quaking

aspen communities are well represented (Ross and Hunter 1976; USDA Soil Conservation Service 1981).

SUB-TROPICAL STEPPE PLAINS ECODIVISION (12)

This is a complex of plateaus and plains lying in eastern New Mexico, northern and central Texas, and southern Oklahoma. The climate is subtropical. Summers are long and hot, with most of the annual precipitation; winters are short and mild. This area has two ecoprovinces, one of which is shown on the map.

Southern Great Plains Ecoprovince

Landforms. Like the Northern Great Plains, this ecoprovince is a high elevation, rolling plain with dissected river valleys. Hills and uplands are common.

Climate. The climate is greatly influenced by the Gulf of Mexico air masses coalescing with the subtropical desert air from the southwest. Much of the precipitation falls in the spring and fall. Due to the high elevation, freezing conditions may occur during the winter and early spring.

Vegetation. Common native vegetation is mixed-oak savanna of live oak, post oak, and blackjack oak, with little bluestem, sideoats grama, switchgrass, plains lovegrass, and plains brittlegrass. Shinnery oak and sand sagebrush grow in the northern portions on sandy soils (Brown 1982c; USDA Soil Conservation Service 1981).

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ECOPROVINCES OF THE CENTRAL NORTH AMERICAN CORDILLERA AND ADJACENT PLAINS

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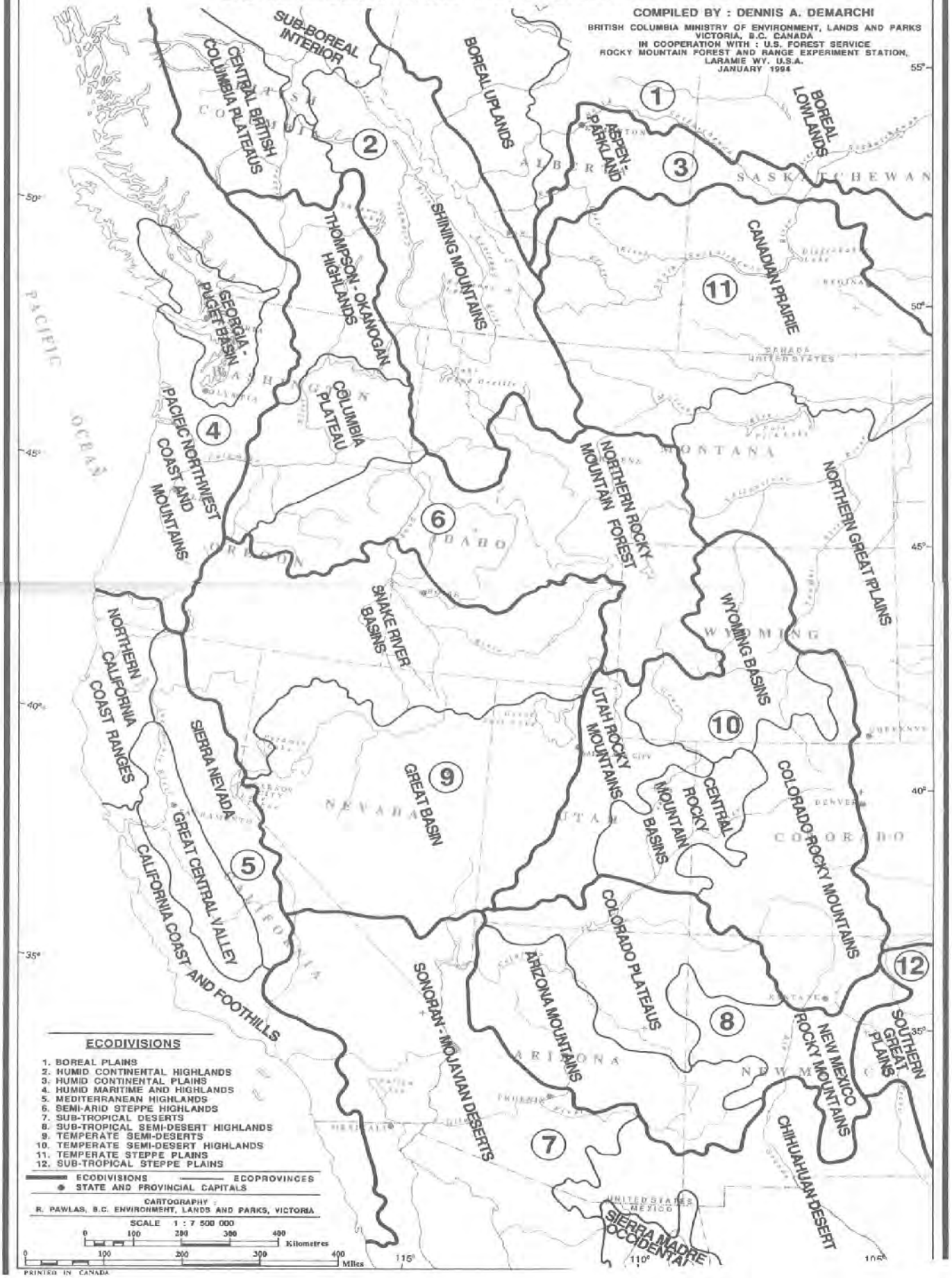
VICTORIA, B.C. CANADA
IN COOPERATION WITH : U.S. FOREST SERVICE
ROCKY MOUNTAIN FOREST AND RANGE EXPERIMENT STATION,
LARAMIE WY. U.S.A.
JANUARY 1994



Appendix B

Fisher, Lynx, Wolverine Summary of Distribution Information

Mary Maj, USDA Forest Service, Northern Region, Missoula, Montana

E. O. Garton, Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho

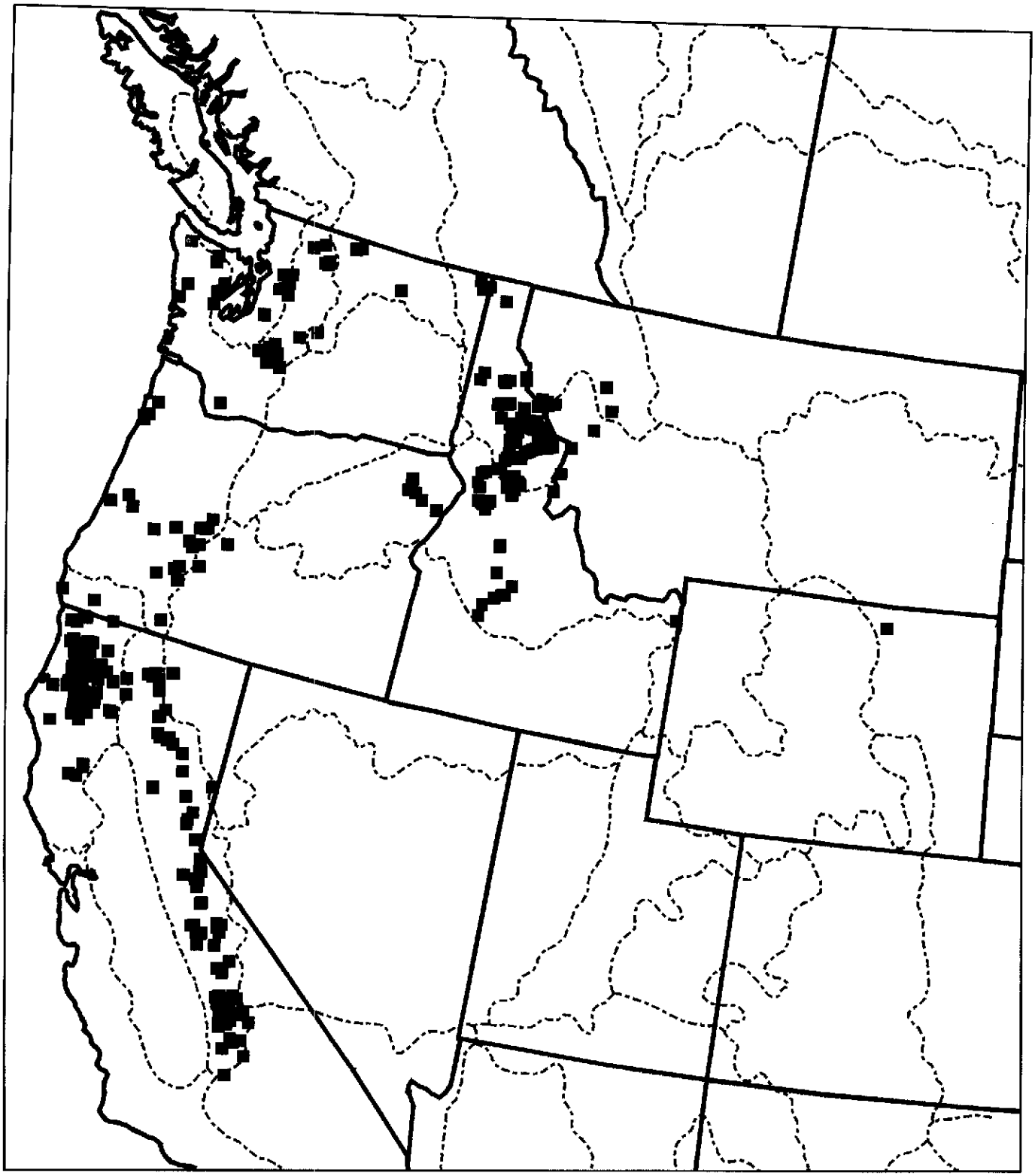
We present maps depicting distributions of fisher, lynx, and wolverine in the western United States since 1961. Comparison of past and current distributions of species can shed light on population persistence, periods of population isolation, metapopulation structure, and important connecting landscapes. Information on the distribution of the American marten is not included because the large number of observations of this species prevented their being analyzed and presented in the same manner as for the other forest carnivores. Dotted lines represent ecoprovince boundaries (see Appendix A).

Records used to create these maps came from state wildlife and natural resource agencies, Natural Heritage data centers, U.S. Department of Agriculture, Forest Service records, and limited published information. All sources were contacted for all records that had dates and could be plotted by legal descriptions or UTM. Verification of each record was preferred but was not a criterion for its use. The records are divided into two time periods within which habitat conditions or harvest pressure from trapping was relatively similar throughout the West: (1) 1961-1982, when the fur market and trapping were very active and widespread habitat modification was starting to occur and (2) 1983-1993, when the greatest extent and intensity of habitat modification occured.

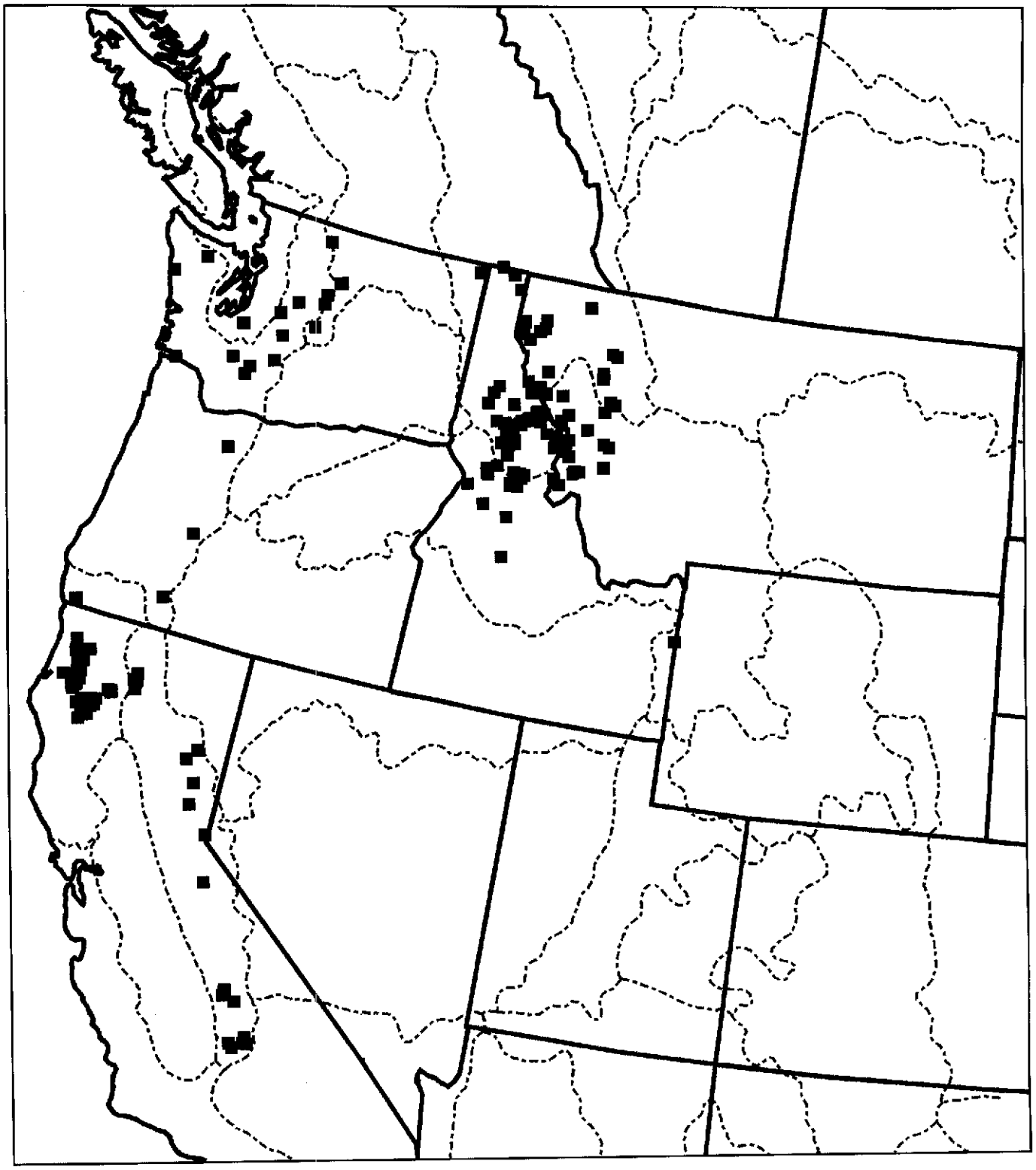
Validation of records varies considerably between states and data bases. Colorado's five-point validation system made it easy to identify and use records classified as "certain" (skull, skin, photo), "highly probable," (tracks by experts) and "probable." We tried to apply the same validation criteria to records where validation from the receiving source was uncertain. All records with uncertain validation were first plotted and then examined according to their relative proximity to other verified points. Because we did not attempt to quantify population density, an error of plotting an invalid record within the distributional range of valid records was not a concern.

It is not appropriate to compare the number of records between time periods and states due to the bias in effort of collecting specimens, documenting observations, and documenting records. As an example, many of the records older than 1983 came from state wildlife harvest data and do not represent an unbiased search for the species over time or geographic area. Demarchi's Ecoregions boundaries (Appendix A) are also shown. The search for information used in creating these maps was not exhaustive; given more time, additional records could be added. A total of 2,316 records were plotted in the creation of these maps. Some individual points represent multiple records. An example is the Montana fisher map, where a reintroduction program resulted in multiple individuals being placed in a single area and plotted as one point.

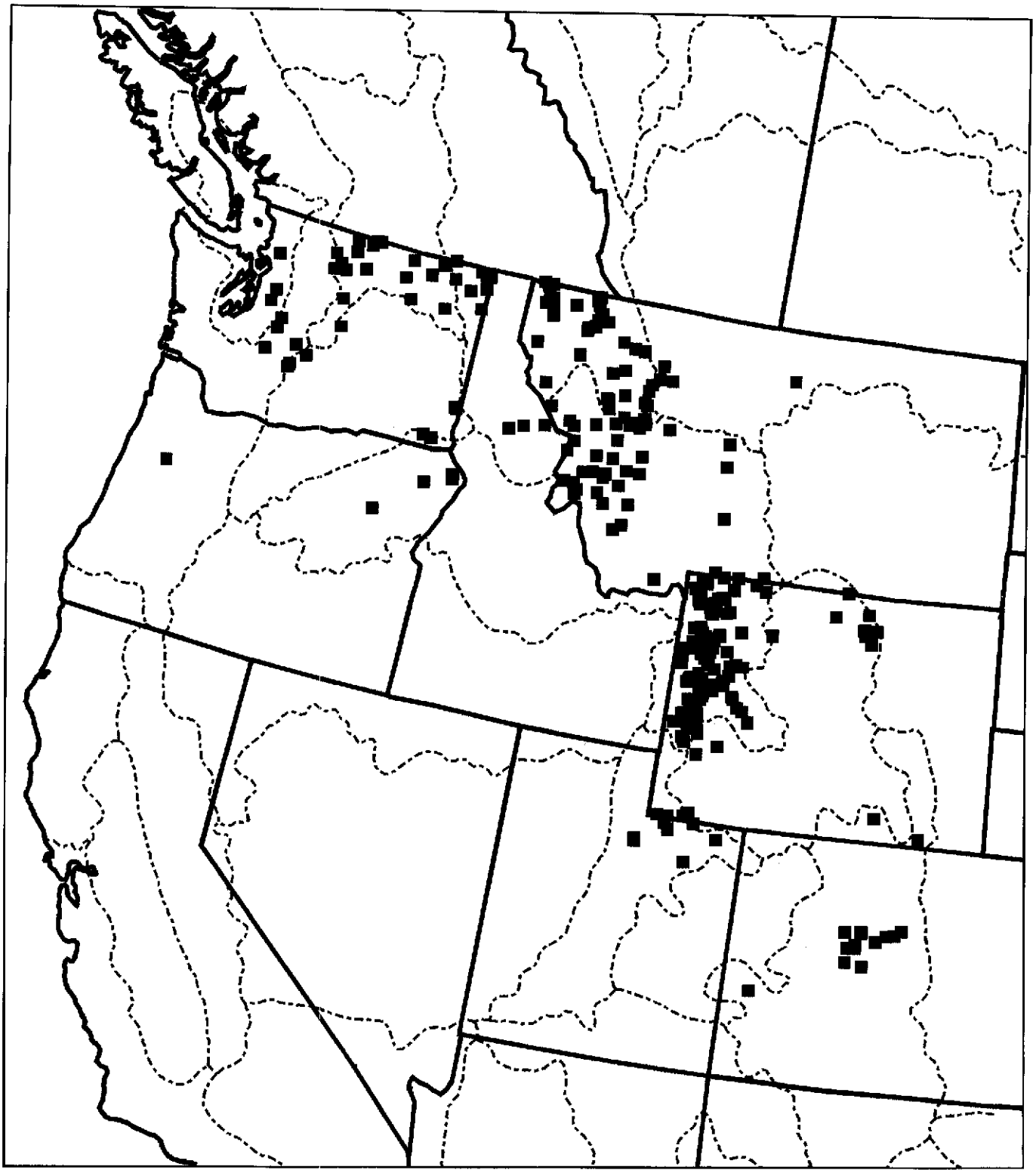
The patterns of occurrence shown in the following maps reflect real ecological forces as well as sampling biases. The general increase in numbers of observations per year from 1961-1982 to 1983-1993 likely reflects increases in physical access to areas where these species can be seen, increasing numbers of people visiting these areas, and improved systems for recording, storing, and retrieving these observations. Jurisdictional (e.g., state) differences in systems of recording and storing observations may account for some of the geographical patterns observed. Still, these maps, interpreted with caution, provide evidence of changing distributional patterns of forest carnivores and support descriptions of such changes that are reported in the species account chapters.



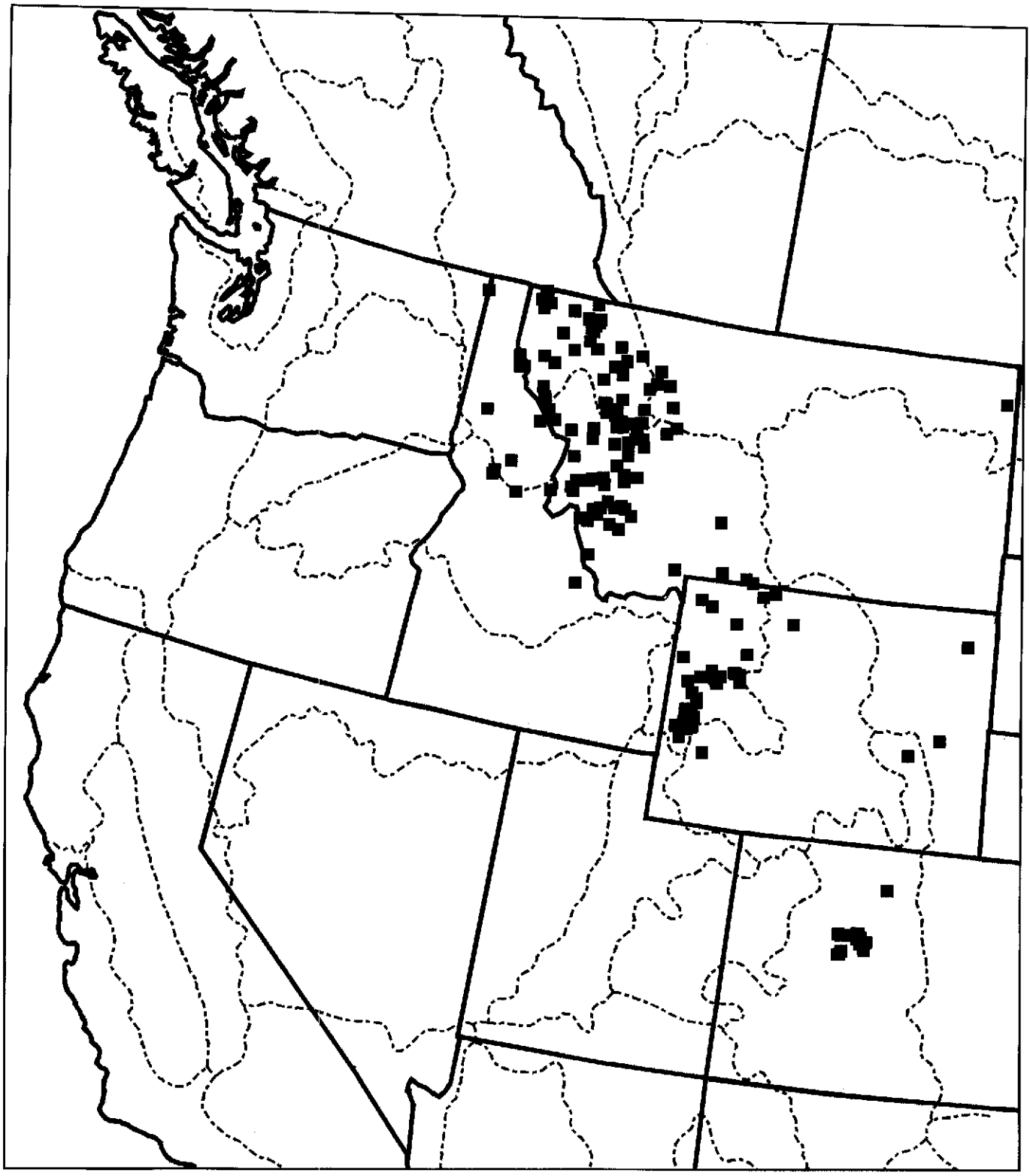
Fisher observations 1961 to 1982.



Fisher observations 1983 to 1993.



Lynx observations 1961 to 1982.



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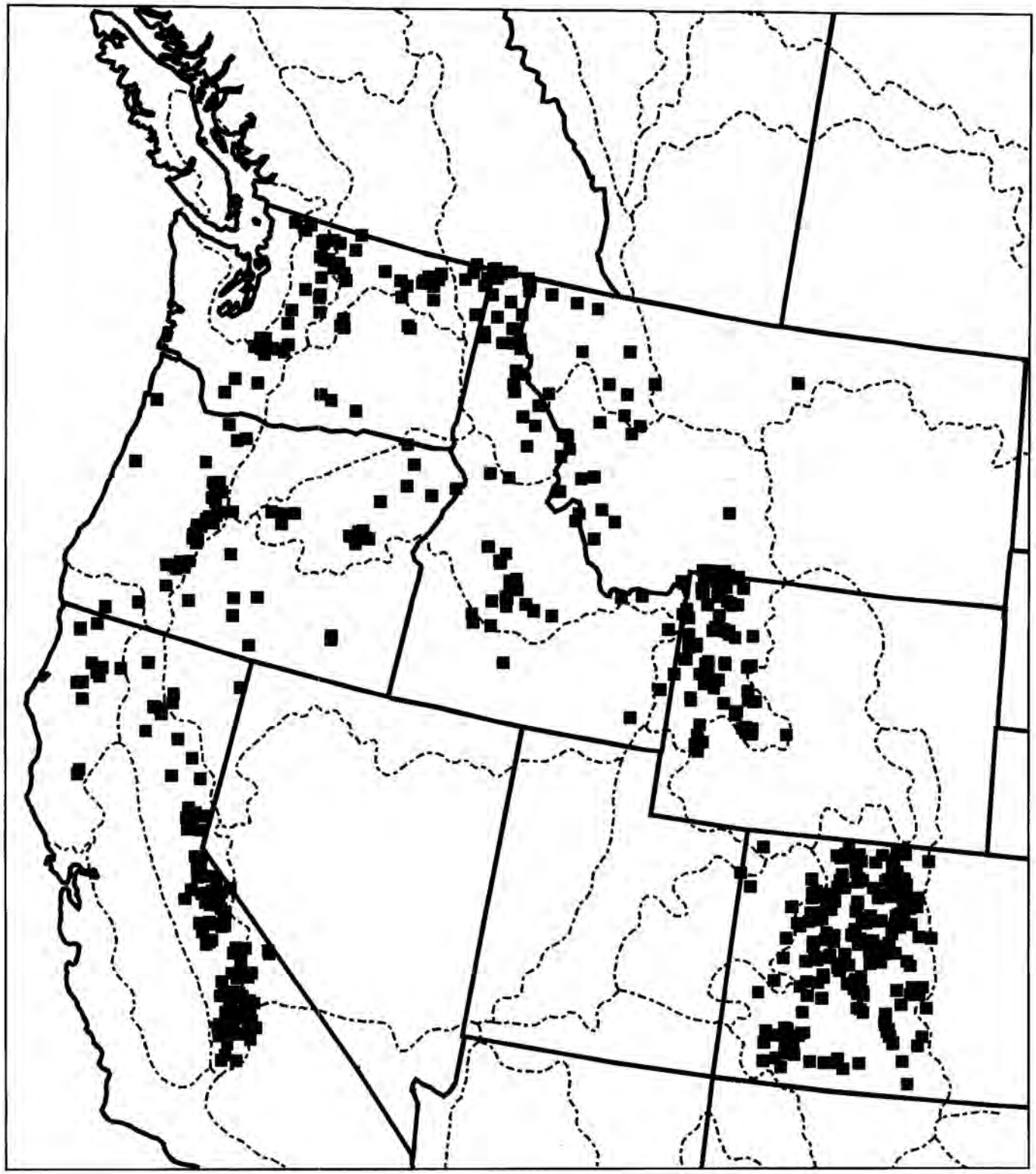
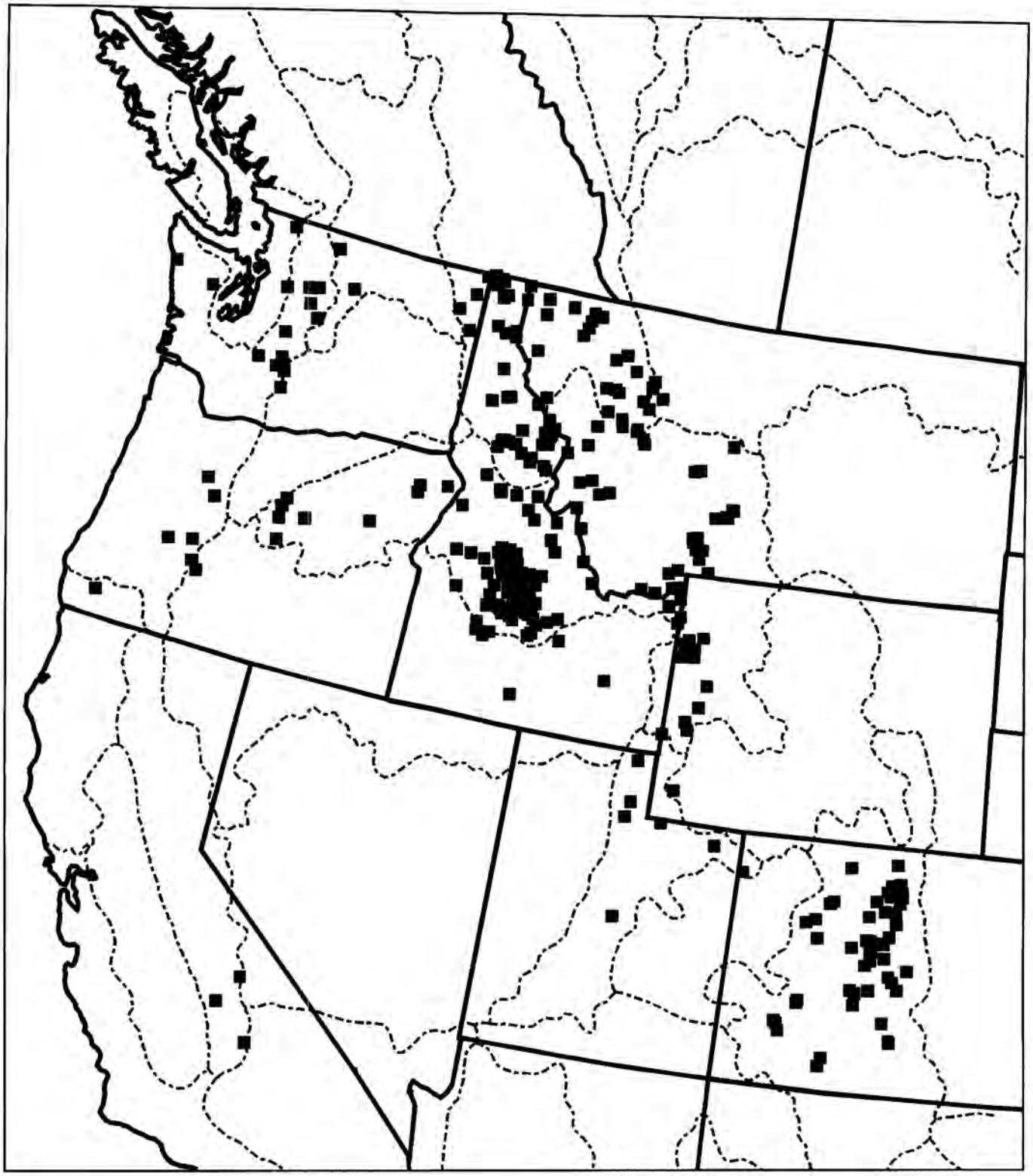


Wolverine observations 1961 to 1982.



Wolverine observations 1983 to 1993.

Appendix C

National Forest System Status Information

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FOREST CARNIVORE DATA FROM NATIONAL FOREST SYSTEM LANDS IN THE WESTERN UNITED STATES

The information presented in this appendix was compiled from responses to two separate forest carnivore questionnaires distributed to Forest Service Regions 1, 2, 3, 4, 5, 6, and 10 in early 1993. Each region designated a primary contact to serve on the Habitat Conservation Assessment Management Team. It was the duty of each representative to provide and verify accuracy of data. Regional Management Team contacts queried National Forest wildlife biologists, state agency biologists, and various affiliated researchers to provide the data for the western Regions that are summarized in the following tables.

These data represent the management situation that existed during the spring of 1993. Because Forest Service habitat management is an ever-evolving process to keep pace with advances in scientific knowledge, portions of this information will be rapidly outdated. Any use or extrapolation of the information presented in this appendix requires subsequent data verification. Nonetheless, we believe this background information contributes to an understanding of the current management situation on lands of the National Forest System in the western United States.

Table 1 presents the status of marten, fisher, lynx, and wolverine on individual National Forests within each Region. A species is considered present if a professional biologist has evaluated the data base and found identification to be conclusive. Care should be exercised in interpreting negative responses. Since absence cannot be proven, the only valid conclusion one may draw is that presence has not been verified on the Forest as of spring 1993. Some Forests chose to respond with "possible" or "unknown at this time" regarding presence. This generally indicates that a Forest lacks verified sightings, although the Forest is within the historic or potential range of the species.

Many National Forests use forest: carnivores to indicate how particular habitats respond to management activities or lack thereof. The Forest Land and Resource Management Plan normally documents status as a Management Indicator Species (MIS). This is noted in the MIS? column. Not applicable (N/A) in the MIS? column is entered where a species has not been documented as present.

Tables 2a-d itemize studies that are complete but not published in the scientific literature or were underway during the spring of 1993. This unpublished "gray" literature has limited availability but still may provide information useful for habitat management. This literature may not have received the intensive peer review necessary to ensure that the conclusions and inferences are thoroughly supported by the data. Should the reader desire to make use of these studies, it is prudent to use only the empirical data provided. This is not to imply that the authors/researchers have erred in their discussion or conclusions in any way, but rather that a possibility exists for an hypothesis to have been overlooked or non-rigorously tested due to limited scientific exposure and scrutiny. Individuals that are familiar with the research listed are identified for the convenience of the reader.

Tables 3a-d summarize the level of public interest in each species within the various NFS Regions. Responses to this question can assist the manager in assessing the social implications of various habitat management approaches and strategies. This information should be weighed in addition to biological considerations when analyzing management effects and possible strategies for the conservation of marten, fisher, lynx, and wolverine.

Finally, Tables 4a-d summarize the administrative status of each of the four species in the western United States by Forest Service Region and state within region. Each species is identified as either Endangered, Threatened, or of Special Concern. The designation of Forest Service "Sensitive," as outlined in the National Forest Management Act, and "Furbearing" status are also included. The latter indicates that the species is commercially trapped. This table complements the tables on "current management status" that are included in each species chapter.

Table 1.-Forest carnivore occurrence (from 1982 to the present) and status on National Forest System lands in the western United States. (Y=Yes; N=No; P=Possible; MU=Management unit; MR=Management requirement species; U=Unknown; MIS=Management indicator species; N/A=Not applicable)

		MARTEN		FISHER		LYNX		WOLVERINE	
Region	National Forest	Presence	MIS?	Presence	MIS?	Presence	MIS?	Presence	MIS?
1	Beaverhead	Y	Y	N	N/A	Y	N	Y	N
	Bitterroot	Y	Y	Y	N	Y	N	Y	N
	Clearwater	Y	Y	Y	N	Y	N	Y	N
	Custer	Y	Y	N	N/A	N	N/A	Y	N
	Deerlodge	Y	N	Y	N	Y	N	P	N
	Flathead	Y	Y	Y	N	Y	N	Y	N
	Gallatin	Y	N	N	N/A	Y	N	Y	N
	Helena	Y	N	P	N	Y	N	Y	N
	Idaho Panhandle	Y	Y	Y	N	Y	N	Y	N
	Kootenai	Y	N	Y	N	Y	N	Y	N
	Lewis and Clark	Y	N	Y	N	Y	Y	Y	Y
	Lolo	Y	N	Y	N	Y	N	Y	N
	Nez Perce	Y	Y	Y	Y	Y	N	Y	N
2	Arapaho-Roosevelt	Y	Y	N	N/A	N	N/A	N	N/A
	Bighorn	Y	Y	Y	N	N	N/A	N	N/A
	Black Hills	Y	N	N	N/A	N	N/A	N	N/A
	Grand Mesa	Y	Y	N	N/A	N	N/A	N	N/A
	Gunnison	Y	Y	N	N/A	N	N/A	N	N/A
	Medicine Bow	Y	Y	N	N/A	N	N/A	N	N/A
	Pike	Y	Y	N	N/A	N	N/A	N	N/A
	Rio Grande	Y	Y	N	N/A	N	N/A	N	N/A
	Routt	Y	Y	N	N/A	N	N/A	N	N/A
	San Isabel	Y	Y	N	N/A	N	N/A	N	N/A
	SanJuan	Y	Y	N	N/A	N	N/A	N	N/A
	Shoshone	Y	Y	N	N/A	N	N/A	N	N/A
	Uncompahgre	Y	Y	N	N/A	N	N/A	N	N/A
	White River	Y	N	Y	N	N	N/A	N	N/A
3	Carson	Y	N	N	N/A	N	N/A	N	N/A
	Santa Fe	Y	N	N	N/A	N	N/A	N	N/A
4	Ashely	Y		N	N/A	N	N/A	N	N/A
	Boise	Y		N	N/A	N	N/A	Y	N
	Bridger-Teton	Y		N	N/A	N	N/A	Y	N
	Caribou	Y		N	N/A	Y	Y	Y	N
	Challis	Y		N	N/A	N	N/A	Y	N
	Dixie	N	N/A	N	N/A	N	N/A	N	N/A
	Fishlake	N	N/A	N	N/A	N	N/A	N	N/A
	Humboldt	N	N/A	N	N/A	N	N/A	N	N/A
	Manti-LaSal	N	N/A	N	N/A	N	N/A	N	N/A
	Payette	Y		Y		N	N/A	Y	N
	Salmon	Y	Y	N	N/A	Y	Y	Y	N
	Sawtooth	Y		N	N/A	N	N/A	Y	N
	Targhee	Y		Y		N	N/A	Y	N
	Toiyabe	Y		N	N/A	N	N/A	Y	N
	Uinta	N	N/A	N	N/A	N	N/A	N	N/A
	Wasatcn-Cache	Y		N	N/A	Y	N	Y	N
5	Eldorado	Y	N	Y	N	N	N/A	N	N/A
	Inyo	Y	N	N	N/A	N	N/A	Y	N
	Klamath	Y	N	Y	N	N	N/A	Y	N
	Lk Tahoe Basin MU	Y	N	N	N/A	N	N/A	Y	N
	Lassen	Y	Y	N	N/A	N	N/A	Y	N
	Mendocino	Y	N	Y	N	N	N/A	N	N/A

(*continued*)

Table 1.-(continued)

		MARTEN		FISHER		LYNX		WOLVERINE	
Region	National Forest	Presence	MIS?	Presence	MIS?	Presence	MIS?	Presence	MIS?
	Modoc	Y	Y	N	N/A	N	N/A	N	N/A
	Plumas	Y	Y	N	N/A	N	N/A	N	N/A
	Sequoia	Y	N	Y	N	N	N/A	Y	N
	Shasta-Trinity	Y	N	Y	N	N	N/A	Y	N
	Sierra	Y	N	Y	N	N	N/A	Y	N
	Six Rivers	Y	N	Y	N	N	N/A	Y	N
	Stanislaus	Y	N	Y	N	N	N/A	Y	N
	Tahoe	Y	Y	Y	N	N	N/A	Y	Y
6	Colville	Y	MR	N	N/A	Y	N	Y	N
	Deschutes	Y	MR	N	N/A	N	N/A	Y	N
	Fremont	Y	MR	N	N/A	N	N/A	N	N/A
	Gifford Pinchot	Y	MR	Y	N	Y	N	Y	N
	Mt.Baker/Snoqualmie	Y	MR	U	N	Y	N	P	N
	Mt. Hood	Y	MR	N	N/A	Y	N	Y	N
	Malheur	Y	MR	U	N	Y	N	Y	N
	Ochoco	Y	N	N	N/A	N	N/A	Y	N
	Okanogan	Y	MR	Y	N	Y	Y	Y	N
	Olympic	Y	MR	U	N	N	N/A	N	N/A
	Rogue River	Y	MR	Y	N	N	N/A	Y	N
	Siskiyou	Y	MR	Y	N	N	N/A	Y	N
	Siuslaw	Y	MR	N	N/A	N	N/A	N	N/A
	Umatilla	Y	MR	U	N	Y	N	Y	N
	Umpqua	Y	MR	Y	N	U	N	Y	N
	Wallowa Whitman	Y	MR	Y	N	Y	N	Y	N
	Wenatchee	Y	MR	Y	N	Y	N	Y	N
	Willamette	Y	MR	Y	N	U	N	Y	N
	Winema	Y	MR	Y	N	Y	N	Y	N
10	Chugach	Y	Y	N	N/A	Y (cyclic)	N	Y	N
	Tongass	Y	Y	N	N/A	Y (cyclic)	N	Y	N

Table 2a.-Unpublished studies conducted on marten.

Region	National Forest	Type of study	Contact person
1	Beaverhead & Gallatin	Habitat use	Jeff Jones or Marion Cherry
2	Black Hills	Introduction/life history	Barry Parrish
3		None	
4	Ashley	Presence/absence surveys	Kathy Paulin
5	Lassen	Habitat use patterns in patchy (logged) environment (1st yr)	Cindy Zabel
	Sierra	Habitat relationships	Steve Laymon
	Six Rivers	Habitat relationships & demographics (in progress)	Bill Zielinski
	Tahoe	Ecology (1980 MS thesis)	Terry Simon-Jackson
		Effects of salvage harvest (in progress)	Sandy Martin
6	Mt. Baker/Snoqualmie	Status reports	Charles Vandemoer
	Olympic	Long-term habitat	PNW[2]-Olympia, WA
	Willamette	ODFW[1] - track, trap, photo	Cory Heath
10	Tongass	Habitat relationships, demographics, ecology	Chris Iverson

[1] *ODFW = Oregon Department of Fish and Wildlife*
[2] *PNW = USDA Forest Service, Pacific Northwest Experiment Station*

Table 2b.-Unpublished studies conducted on fisher.

Region	National Forest	Type of study	Contact person
1	Kootenai	Habitat use and dispersal	Bob Summerfield
		Population augmentation	Jeff Jones
2		None	
3		Does not occur	
4		None	
5	Sequoia	Habitat relationships and competition with marten (in progress)	Bill Zielinski
	Shasta-Trinity	Habitat use-telemetry to test validity of R5 survey protocol	Rick Golightly
	Six Rivers	Habitat relationships-telemetry	Bill Zielinski
6	Mt. Baker-Snoqualmie	Status reports	Charles Vandemoer
10		Does not occur	

Table 2c.-Unpublished studies conducted on lynx.

Region	National Forest	Type of study	Contact person
1		None	
2		None	
3		Does not occur	
4		None	
5		Does not occur	
6	Mt. Baker-Snoqualmie	Status reports	Charles Vandemoer
	Okanogan	6-Year research	Bob Naney
10		None	

Table 2d.-Unpublished studies conducted on wolverine.

Region	National Forest	Type of study	Contact person
1		None	
2		None	
3		Does not occur	
4	Boise	Ecology and demographics	John Erickson
	Challis	Ecology and demographics	Dave Reeder
	Sawtooth	Ecology and demographics	Howard Hudak
5		None	
6	Mt. Baker-Snoqualmie	Status reports	Charles Vandemoer
	Mt. Hood	Literature search	Barb Knott
10		None	

Table 3a.-Level of public interest in the Forest Service's management of marten habitat.

Region 1	Listing as Forest Service Sensitive has heightened public awareness, and marten are tied to the old-growth forest issue.
Region 2	Currently, marten are not a significant issue on any Forest in Region 2, It is often raised as an issue during public scoping at the project level for several Forests. Marten is generally included in a long list of species that may have connections with habitat fragmentation or forest practices. No appeals or litigations specific to marten have been recorded at this time.
Region 3	Marten habitat management is not a major issue in the Region. The species occurs on only 2 Forests --- the Carson and Santa Fe, It has not been an appeal issue. In the Forest Land and Resource Management Plans for these two Forests, marten was an issue as one of several sensitive species mentioned. It is occasionally mentioned in letters to these Forests and was raised as an issue in one timber sale on the Santa Fe that was eventually dropped from consideration.
Region 4	The Salmon National Forest has had one appeal on one timber sale, No other Forests have been appealed on marten-related issues,
Region 5	Within the last 7 years, there have been 45 appeals, one lawsuit, and 12 Freedom of Information Act (FOIA) requests for information that have dealt with marten. The concern of the public is evident by the high profile of this species in California as well as by the 58 actions listed above.
Region 6	The greatest point of contention appears to be the effectiveness of the "Management Requirement" concept with respect to maintaining population viability over time. The Natural Resources Defense Council takes issue with our approach. Many forest plan appeals were filed. Appeals challenged the marten population estimates as well as timber rotation lengths necessary to meet marten life history/habitat requirements. Many concerns were expressed regarding the effects of management on populations and distribution.
Region 10	Tongass National Forest - Timber harvest directly affects preferred habitats; open roads result in Increased trapping pressure, The issue has been raised consistently during Forest-wide and project-level planning for both subsistence and sport trapping.
	Chugach National Forest - Spruce bark beetle infestations have resulted in changing habitat composition and structure. The effects of the infestation and subsequent management practices may affect marten habitats and populations. The issue has been raised during project planning.

Table 3b.-Level of public interest in the Forest Service's management of fisher habitat.

Region 1	Listing the fisher as Forest Service Sensitive has heightened public awareness of this species.
Region 2	Occurring only in the state of Wyoming, the fisher does not seem to be much of an issue.
Region 3	Fisher do not occur in New Mexico or Arizona.
Region 4	There appears to be little concern for fisher. There have been neither appeals nor litigations at the project or Forest planning levels.
Region 5	Within the last 7 years, there have been 41 appeals, one lawsuit, and 12 Freedom of Information Act (FOIA) requests for information that have dealt with fisher. The concern of the public is evident by the high profile of this species in California, as well as by the 54 actions listed above, The Pacific subspecies was petitioned for federal listing under the Endangered Species Act, but the petition was denied largely due to lack of information.
Region 6	Fisher habitat has not been a MAJOR issue, with the limited exception of some southern Oregon Forests.
Region 10	Fisher do not occur in Alaska.

Table 3c.-Level of public interest in the Forest Service's management of lynx habitat.

Region 1	Listing the lynx as Forest Service Sensitive has heightened public awareness.
Region 2	Currently, lynx have not been a significant issue on any Forest. It has been raised as an issue during public scoping at the project level for several Forests: the Routt, San Juan, and White River. These were ski area development or expansion projects. Lynx habitat management was mentioned during pre-appeal discussions on the Lake Catamount Ski Area
	Environmental Impact Statement but was not included in the final appeal.
Region 3	Lynx do not occur in New Mexico or Arizona.
Region 4	There appears to be little public concern for lynx. There have been no appeals or litigation concerning this species during project National Environmental Policy Act (NEPA) analysis or Forest land management planning.
Region 5	Lynx do not occur in California.
Region 6	In north-central Washington, the issue of both federal and state status has been large. Effects of management in general, road construction in particular, and entry into roadless areas have been hotly debated.
Region 10	Formerly a U,S. Fish and Wildlife Service Category 2 species, there is currently an open trapping season on both Forests. Public concern appears limited.

Table 3d.-Level of public interest in the Forest Service's management of wolverine habitat.

Region 1	Listing as Forest Service Sensitive has heightened public awareness.
Region 2	Currently, the wolverine has not been a significant issue on any Forest. It has been raised as an issue during public scoping at the project level for several Forests: the Routt, San Juan, and White River. These were ski area development or expansion projects. Wolverine habitat management was mentioned during pre-appeal discussions on the Lake Catamount Ski Area EIS but was not included in the final appeal.
Region 3	Wolverine do not occur in Arizona or New Mexico.
Region 4	The Sawtooth National Forest Land and Resource Management Plan was appealed based on failure to display the effects of off-road vehicle (ORV) use and timber management activities on wolverine. No other Forest in Region 4 has been appealed concerning this species.
Region 5	Within the last 7 years, the Region has had 14 appeals and 6 Freedom of Information Act (FOIA) requests for information that have dealt with wolverine. The concern of the public is evident by the 20 actions listed above. Although maintaining a lower profile than either fisher or marten, the wolverine has the potential to become a major issue once presence can be verified on Forests in the Region. The Region also invested roughly $40,000 in the California Cooperative Wolverine Study over the last two years. This study employs remote infra-red triggered cameras placed over bait in the winter to obtain photo documentation of species' presence,
Region 6	Wolverine have been an appeal point on several environmental assessments. Concerns included maintaining population viability, entering roadless areas (reducing refugia), lack of information (especially population and distribution), habitat use, and lack of conservation measures.
Region 10	Wolverine habitat management is not an issue.

Table 4a.-Status of marten in the western United States. ^{R}= Reintroduced population; MR = Management requirement species; S = Forest Service sensitive.

Region	State	FS	State endangered	State threatened	State Species of special concern	Furbearing
1	Idaho					X
	Montana					X
2	Colorado	S				X
	South Dakota	S				X^{R}
	Wyoming	S				X
3	New Mexico	S	X			X
4	Idaho	S				X
	Nevada	S			No Season	X
	Utah	S			X	
	Wyoming	S				X
5	California	S				
6	Oregon	MR			Sensitive	
	Washington	MR				X
10	Alaska					X

Table 4b.-Status of fisher in the western United States. The Pacific fisher is a federal C2 species in California, Oregon, and Washington. A C2 designation indicates that more information is necessary before a listing decision can be made by USFWS. RH = Restricted Harvest; S = Forest Service Sensitive; N/A = Not Applicable.

Region	State	FS	State endangered	State threatened	State species of special concern	Furbearing
1	Idaho	S			X	
	Montana	S				X, RH
2	Colorado	S	No records			
	South Dakota	S	No records			
	Wyoming	S			"Protected"	
4	Idaho	S			X	
	Nevada	N/A				
	Utah	S		X(Extirpated)		
	Wyoming	S			X	
5	California	S			X	
6	Oregon				Sensitive	
	Washington		Candidate	Candidate		Candidate Sensitive

Table 4c.-Status of lynx in the western United States. The lynx is a federal C2 species in AK, CO, ID, MT, NV, OR, UT, WA, and WY. A C2 designation indicates that more information is necessary before a listing decision can be made by USFWS. RH = Restricted Harvest; S = Forest Service Sensitive.

Region	State	FS	State endangered	State threatened	State species of special concern	Furbearing
1	Idaho	S			X	
	Montana	S				X, RH
2	Colorado	S	X			
	South Dakota	N/A				
	Wyoming	S			“Protected”	
4	Idaho	S			X	
	Nevada		No records			
	Utah	S			X	
	Wyoming	S			X	
6	Oregon	S				
	Washington	S		X		
10	Alaska					X

Table 4d.-Status of wolverine in the western United States. *Gulo gulo luscus* is a federal C2 species in CO, ID, MT, NV, UT, and WY. *Gulo gulo luteus* is a federal C2 species in CA, OR, and WA. A C2 designation indicates that more information is required by USFWS prior to a listing decision. RH = Restricted Harvest; S = Forest Service Sensitive.

Region	State	FS	State endangered	State threatened	State species of special concern	Furbearing
1	Idaho	S			X	
	Montana					X, RH
2	Colorado	S	X			
	South Dakota	N/A				
	Wyoming	S			"Protected"	
4	Idaho	S			X	
	Nevada	S	Old records	No status		
	Utah	S			X	
	Wyoming	S			X	
5	California			X		
6	Oregon	S		X		
	Washington	S				X
10	Alaska					X

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins,CO 80526