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 behavioral 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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