The Evolution of Wilderness Wildlife Research in North America

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Abstract—Most wildlife research in North America has focused on a standard suite of questions, asked of a limited assemblage of economically important species and studied using a relatively limited set of techniques, study site characteristics and narrow time-frames. We describe why these factors are not necessarily conducive to conducting wildlife research in wilderness settings. As a consequence, the amount of wildlife research conducted in wilderness settings has historically been small and limited primarily to wilderness-dependent species. We further describe the reasons for this, recent trends and the types of wildlife research questions that can best be addressed in wilderness settings.

Humans, as we define the species, have lived in intimate association with other animals for at least the past 200,000 years, serving as both predator and prey. For all but a small part of this time, they lived in what contemporary terms would call a wilderness environment. The constant interactions with animals, as predators and prey, forced the human species to become knowledgeable about attributes of animal biology and behavior. Knowledge was accumulated and passed down to succeeding generations. Learning the habits of the large game animals and carnivores was probably a true trial and error process. Natural selection played an important role since the trials were often life-threatening and the errors often fatal (Shepard 1973).

Human knowledge of animal behavior and the efficiency of methods to harvest wild animals continued to increase with the size of human populations. As a result, by the dawn of what is usually recognized as civilized culture—ca 5,000 - 7,000 years ago in southern Europe and the Mideast but much later in North America—many of the larger game species had been driven to extinction or were greatly diminished in abundance (Fagan 1989). When and where this occurred, human populations were forced to cease their nomadic ways and develop an agricultural lifestyle that relied on crops and recently domesticated animals. With this shift in lifestyle, the first permanent communities appeared (Gray 1993). As a consequence, the "wilderness quality" of the living environment diminished.

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One consequence of permanent settlement in ever larger communities was that innate knowledge of the ways of wild animals - essential for human survival over the eons but never recorded - became less important and was gradually lost (Shepard 1973). The more civilized Western society became, the more isolated the average person was from wild animals; by the 1600s, western European urban populations had little chance of encountering wild animals, and they could no longer be assured of even eating meat from any source.

With the later gradual evolution of a privileged/leisure class in society in the 18th and 19th centuries, interest in the natural history and taxonomic classification of wild animals increased. This interest was spawned in part by the global expeditions of explorers which awakened the Western world to the diversity of life on the planet (Borland 1975).

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Despite the long history of human involvement with wildlife, it was still not until the early 1900s that an interest in the *actual study* of wildlife began to blossom in North America. The American Game Protective and Propagation Association, a group largely made up of sportsmen, conservationists and sporting arms industry representatives that supported the conservation of game through laws and breeding programs, was instrumental in this effort (Greeley 1931). Initial studies were largely descriptive, based primarily on experience or opinion, lacking data and facts and essentially weak in scientific rigor. This was largely because investigations into the habits of wild animals were typically motivated and supported by various special interest groups. For example, state game departments were primarily interested in satisfying the demands of those who paid for hunting licenses, while universities and federal departments focused on the problems of poultry and livestock to the exclusion of wild bird and animals (Allen 1932).

However, through the discussions and papers presented at the annual American Game Conferences in the early 1900s and continuing in 1936 with its successor, the North American Wildlife Conference, the character of wildlife studies slowly began to change. Although revolutionary at the time, the idea that scientific research was important and could enhance the management of wildlife slowly became accepted and was formally adopted in the American Game Policy of 1930 (Leopold 1930). Beginning in 1935, Cooperative Wildlife Research Units were established at U.S. land grant universities to educate wildlife biologists, conduct research and better integrate state, federal and university

research programs. Enactment of the Federal Aid to Wildlife Restoration Act of 1937 provided the first legal recognition that wildlife management research was necessary and desirable.

Since the 1930s, research on wild animals, principally game animals, in North America has increased tremendously. Consequently, over the past half-century, scientists have learned a great deal about the biology, behavior and ecology of many species. There have been substantial changes and improvements during this time in the methods and analyses wildlife researchers have employed in their attempt to describe the biological characteristics of a given species.

However, there is much we do not know. This has led to speculation about the kinds of species that have been studied and where. We hypothesized that most studies have been conducted on species that are relatively common, have an economic importance either as game or for fur, or pose economic impacts because of damage to agricultural crops, depredation, or disease. We also hypothesized that the common study site is generally convenient, easily accessible by motorized vehicle, and amenable to the use of a variety of equipment and methods. We were also interested in the kinds of questions that biologists have typically asked about wildlife and about what factors have structured those questions. We suspected that over the history of contemporary wildlife research, biologists have asked a relatively limited suite of questions about wildlife, and that the same questions have been asked about the same species over and over again, varying only in the specific location/habitat of the particular study. For example, there have been 634 studies of white-tailed deer conducted in the U. S. and published in the *Journal of Wildlife Management* over the past 60 years, many asking the same questions and differing only in the location of the study.

Finally we suspected that the techniques and methods used to answer these questions, and the kinds of species that are typically involved, have resulted, we believe, in a relatively standard type of research design and that this design could have a strong influence on whether or not wilderness areas are selected for a specific research project. We therefore undertook a series of analyses to categorize the kinds of species studied, the research questions asked, and the research design used.

An Analysis of the Role of Wilderness Areas in Wildlife Research

We examined the role of wilderness areas in the scientific study of wildlife by analyzing the kinds of wildlife species studied over time, the type of environment where study was conducted, that is, in disturbed or human manipulated versus wilderness settings, and where possible, the spatial extent of the study sites. We also sought to characterize the questions or hypotheses the research addressed. In addition, we used the results of a survey by Pelton and Van Manen (1996) that summarized the duration of wildlife studies. (Note: In this paper, we use the term wilderness to refer to large, undisturbed natural areas—"wilderness" with the small "w" as in Schoenfeld and Hendee (1978)—rather than limit it exclusively to legally designated areas).

Methods Used in the Analysis

We defined wildlife broadly, in conducting this analysis, including all terrestrial mammal and avian species native to North America. We used articles published in the *Journal of Wildlife Management* (published from 1937 to the present) the *Wildlife Society Bulletin* (published from 1973 to the present) and *Conservation Biology* (published from 1987 to the present) to document the research studies that have taken place on the various species. We arbitrarily divided the research record into five year increments (with the exception of the first segment), starting in 1937 and continuing to the present, resulting in 13 time periods. For each time period, we examined and categorized every entry in the journals. We limited our analysis to articles that pertained to species of wildlife, eliminating articles that pertained to habitat improvement, analytical techniques and policy. In doing so, we utilized an overall average of 85% of articles published in each of the time periods in the wildlife journals and 7% of the articles published in each time period in *Conservation Biology*.

We grouped species into eight categories, based in part on ecological function, appearance, habitat requirements and human use, recognizing that any subdivision of this sort is arbitrary. These categories and the most common species included are listed at the bottom of table 1. We evaluated each study as to whether it took place in or out of a wilderness environment and attempted to determine the size of the study area. The former evaluation was often subjective because of the lack of a definitive site description. We tried to be conservative and, when in doubt, allocated a study to the wilderness category, when in actuality it may not have taken place in a wilderness environment. Finally, we characterized the primary research questions addressed in each of the studies.

To test for significant trends from 1937 to the present, we evaluated the proportion of studies in five-year increments using multiple regression (Zar 1996). Significance level was set at a=.05.

Assumptions Made in the Analysis

The *Journal of Wildlife Management* and its sibling publication, *The Wildlife Society Bulletin*, are the oldest refereed forums that report on North American wildlife issues. We assumed that these publications represented a valid sample of wildlife research in North America. To evaluate the thoroughness of the coverage of the subject matter encompassed by these journals, we examined the citations of all refereed journals contained in a college textbook on the history of wildlife management in North American (Peek 1986). We found that 49.7% of all journal citations contained in this book are from these two sources alone, and the remaining 50.3% are scattered among 42 different journals. In order to include the growing research emphasis in the field of conservation biology, we also surveyed all articles in

Table 1—Proportion of studies devoted to various mammal and bird species groups published in the *Journal of Wildlife Management* and the *Wildlife Society Bulletin* at five-year intervals between 1937 and 1996, and *Conservation Biology* between 1987 and 1996.

Category	1937	1941	1946	1951	1956	1961	1966	1971	1976	1981	1986	1991	1996
Game birds[1]	38	21	28	28	35	34	21	16	17	14	10	8	10
Waterfowl[2]	19	8	11	17	24	12	21	20	25	21	20	16	21
Songbirds and woodpeckers[3]	4	3	8	2	1	3	-	3	5	5	13	11	13
Raptors, owls and wading birds[4]	-	-	-	-	-	-	-	-	-	7	6	15	11
Large herbivores[5]	11	29	13	24	21	18	35	37	31	30	28	30	23
Small & medium sized mammals[6]	27	39	40	26	17	29	22	17	17	12	15	11	11
Bears[7]	-	-	-	-	-	2	2	4	2	5	3	3	5
Carnivores[8]	-	-	-	2	1	2	-	1	3	4	6	6	10
Number of studies analyzed	26	38	47	46	66	59	105	101	145	182	192	163	171

([1]pheasant, quail sp., grouse sp., woodcock, dove; [2]many different species with mallard and geese dominant; [3]red-cockaded woodpecker dominant; [4]bald eagle dominant; [5]white-tailed deer, mule deer, black-tailed deer, moose, pronghorn antelope, caribou, mountain sheep, bison, mountain goat, elk; [6]muskrat, cottontail rabbit, squirrel sp., coyote, raccoon, fox sp., beaver; [7]grizzly, black and polar bears; [8]wolf, mountain lion, bobcat, lynx)

the identified time periods in the journal *Conservation Biology*. We also examined all articles published from 1951 to the present in the *Journal of Mammalogy*, and the *Canadian Journal of Zoology*, We concluded that the majority of the research reported in these journals was more laboratory oriented and was not appropriate for this study.

We recognize that many studies, such as those conducted by scientists in areas like national parks, are never published in the refereed literature (Wright 1990). However, in most cases, evaluation has shown that these efforts do not constitute a true "research" study, but are rather simple surveys or monitoring efforts (Wright 1990).

Results of the Analysis

The proportion of studies devoted to the eight categories of animals is shown in table 1, grouped in five-year increments. The analysis included a total of 1,343 studies. For the first 30 years of the period analyzed (1937-1966), studies of game birds - particularly quail species and pheasant - were quite common, as were studies of medium-sized mammal species such as muskrat and cottontail rabbit. The number of studies in both of these categories declined appreciably over the next 30 years (1967-1996) as the research focus and probably funding appeared to change. Over the next 30 years, studies of breeding birds, such as the red-cockaded woodpecker in forested environments, and of habitat use by bear and carnivores increased. Studies of waterfowl and large herbivores were relatively constant over the entire time period, and no trend in changes in species composition was detectable over the time period.

We found no significant trend or change in the proportion of studies performed on large herbivores and waterfowl. A significant decrease in the proportion of studies for small mammals (p=.0003) and gamebirds (p=.0003) was noted. A significant increase in the proportion of studies for carnivores (p=.0002), bears (p=.0001) and songbirds (p=.0037) was found by using multiple regression analysis.

The proportion of all studies in each time period considered done in a wilderness environment are shown in table 2. The results suggest that there has been limited use of wilderness settings for wildlife research. This was particularly true in the first 30 years of the record. Over the past 30 years, as the data illustrate, there has been a gradual increase in the use of wilderness settings for wildlife research. Most of this has been on what we define below as wilderness-dependent species.

There is a great diversity in the types of wildlife projects reported in the journals that were surveyed. Approximately 25% of the publications analyzed over the time period were what we considered to be traditional field studies on a defined land area(s). Our determination of the spatial extent of these study sites was subjective because the sizes of the study areas and/or plots were not reported in many cases. We determined that about 18% of the field studies over the entire time period took place in an area >1,000 ha. Over the past 25 years, there was an increase to about 28% of the studies using areas >1,000 ha. Perhaps the increase in proportion of studies on larger tracts of land is due to the increase in the study of species requiring larger tracts of land, such as bears, mountain lions and wolverines.

Although in some cases it was difficult to categorize a given study, we did find that in general, the types of questions

Table 2—Proportion of studies of all animal groups listed in table 1 that were conducted in a wilderness environment. Results are reported at five-year intervals between 1937 and 1996.

Category	1937	1941	1946	1951	1956	1961	1966	1971	1976	1981	1986	1991	1996
Wilderness settings	0	3	4	4	5	6	8	10	8	8	10	10	11

biologists typically asked in wildlife studies was rather limited. Three general types of questions appear to prevail in the literature as determined from our analysis. About 26% of the studies involved examinations of animal food habits and food availability, 24% of the studies involved some form of habitat relationship or habitat use, and 23% of the studies involved the population dynamics of a given species.

Does Wilderness Have a Role in Wildlife Research?

Although the use of wilderness areas for wildlife research has been increasing in recent years, our analyses suggest that the overall use of wilderness areas for research is and has been limited. If this is true, the question is why? We raise this question in the light of the fact that wilderness areas have been touted as research centers, and because of the statement made in the paper on wildlife research in wilderness areas presented at the previous wilderness research conference (Starkey and Larson 1985), which stated that "Wilderness and National Park areas have historically provided excellent study areas for wildlife research."

The reasons appear to be that most wildlife studies have been conducted on species that are relatively common in a variety of non-wilderness landscapes, have an economic importance either as game or for fur or pose economic impacts because of damage to agricultural crops, depredation or disease. Many of these species are generally not found in abundance in most wilderness areas, but thrive in prairie, wetland, riparian and lowland forest habitats, which have not been included in wilderness because of their economic value for agriculture, livestock production and timber. Small game, upland birds and furbearers are also not high priorities for research in national parks, where hunting and trapping is prohibited (Garrett and Wright 1999).

The more recent increase in studies of breeding birds, such as the red-cockaded woodpecker in forested environments, seems to reflect, among other things, increased concerns over the adverse impacts of forest timber management practices (Conner and Rudolph 1991). The more recent increases in studies of habitat use by bears, carnivores and some breeding birds may reflect research projects spawned by the Endangered Species Act (Johnson 1979). It seems likely that this trend will continue.

Wilderness settings provide habitats that receive a minimal amount of human disturbance while providing the opportunity for natural disturbance and ecological processes to operate with minimal human interference (Starkey and Larson 1985). However, the price of maintaining undisturbed environments includes restrictions on use and access. We speculated that in planning a field research project, most researchers select study sites that are generally convenient to use, are easily accessible by motorized vehicle and amenable to the use of a variety of equipment/methods. This is often done to simplify logistics and limit expenses. The restrictions associated with wilderness typically complicate logistics and increase the expenses of doing research. It appears that many scientists have found it either not necessary, are not willing or simply cannot afford to work in wilderness settings unless the species of interest requires it.

The large spatial extent of most wilderness areas is generally considered an important attribute to some types of research because, among other things, it can provide a buffer against surrounding fragmentation and habitat disruption. However, our analysis has shown that the use of large study areas in research projects is uncommon. Some investigators have speculated that many biologists simply may not be comfortable working at large ecological scales (May 1994). In fact, the focus of most ecological studies has long been on relatively small spatial units, with the $1m^2$ plot being the dominant unit of analysis, and most ecological theory has developed from studies conducted on small spatial units (Kareiva and Anderson 1989). The story that seems to emerge is that the use of large undisturbed environments for study sites may have little attraction for most wildlife biologists. This factor clearly ties into the restrictions on access discussed above. However, over the past 25 years, there has been an apparent increase in the spatial scale of some analyses and a higher proportion of studies conducted in larger areas (i.e. >1,000 ha). This trend appears to be reflective of the overall increase in studies of wilderness-dependent species shown in table 2.

Wildlife biologists generally acknowledge that understanding the ecological complexities of natural environments typically requires long-term studies (Halvorson and Davis 1996). However, these are uncommonly rare in North America, particularly for the study of wildlife, even though there seems to be a universal appreciation of long-term studies. Pelton and van Manen (1996), in a survey of wildlife studies published in the *Journal of Wildlife Management,* found that 80% of the wildlife studies were based on <5 years data, and 65% were conducted over three years or less, which is generally the time period of a graduate student research project. The typical funding cycles for most research studies, combined with the need for quick results, create a strong disincentive for long-term study (Weatherhead 1986) and again may mitigate against using environments where logistic and ecological complexities may, of necessity, extend the duration of the study.

Wilderness Dependent Species

We believe it is unlikely that many of the factors described above will change in the near future. Consequently, we do not believe that wilderness areas are likely to be a setting for the study of the majority of wildlife species. Rather, the focus of research in wilderness areas will likely continue to be species that may be considered wilderness-dependent (Schoenfeld and Hendee 1978) - not because they require wilderness habitats per se, but because they require wilderness to avoid conflicts with humans and to decrease their vulnerability to human-caused mortality (Mattson 1997). Thus, while grizzly bears may tolerate the habitat disturbance associated with some forms of logging, they generally cannot tolerate the increases in human densities and activities associated with logging. In other words, for a species like grizzly bear, wilderness primarily represents an environment with few humans, where, as a consequence, it can find refuge.

In defining wilderness-dependent species in this manner, we exclude the many species that, for one reason or another, may at times conflict with humans and their use of the land.

Beaver in suburban drainages, geese on golf courses, coyotes on sheep ranches and birds in orchards are but a few examples of human/wildlife conflicts. There are likewise many species that may at times be vulnerable to human-caused mortality but whose population is little affected. Currently over 50,000 white-tailed deer are killed each year on Pennsylvania highways, yet the population has been unaffected. Instead, we focus on a far smaller number of species that can, if habitat conditions permit, come into constant conflict with humans *and* are usually vulnerable at all times to human mortality. For these species, wilderness offers both refuge and often the only possible place to study them.

Species falling into this category generally share three distinct biological characteristics (Mattson 1997):

1. They tend to be large, with relatively low rates of fecundity and therefore low potential population growth rate, thus making them more vulnerable to extirpation than populations of small animals with high reproductive potential.
2. They are more likely to be killed by humans because they pose a threat to humans or their property.
3. They may display behavioral traits such as aggressiveness that can make them a threat to human safety, thus predisposing them to lethal responses.

The anthropocentric threats faced by such species are ironic, considering the fact that surveys have shown that there is strong public support for the protection of these wilderness wildlife species (Kellert 1984). However, it seems indisputable that protection from human-caused mortality is primary to the survival of wilderness-dependent wildlife. Yet despite rigorous protection by federal endangered species laws, virtually all grizzly bears and wolves that die in the U. S. are killed by humans (Mattson and others 1996). Most of these deaths occur outside of national park wilderness areas, and many occur because humans are armed, often in the pursuit of game species, and perceive themselves to be threatened. Therefore, wilderness designation alone cannot guarantee the preservation of such species.

To summarize, we have provided an overview of wildlife research in North America, pointing out that although wilderness areas seem to be nonessential for a majority of studies on the majority of species, they are essential for furthering our understanding of wilderness-dependent species. In making this statement, we do not mean to imply that wilderness areas are not important baselines against which to monitor factors impacting wildlife in non-wilderness situations (Peek 1980). Because of this and other factors, we also do not want to imply that the present situation—of a relatively low proportion of wildlife studies conducted in wilderness areas—is necessarily desirable.

In the following sections, we present an overview of contemporary research on selected wilderness-dependent wildlife species, focusing on the questions that are being asked and seeking to determine whether wildlife research in wilderness areas can help us better answer them. In this overview we focus on wolverines (*Gulo gulo*), mountain lions (*Felis concolor*), grizzly bears (*Ursus arctos horribilis)*, wolves (*Canis lupus*) and lynx (*Lynx rufus*).

Wilderness Research and Wolverines

The wolverine is characterized as one of North America's rarest mammals and least understood carnivores (Banci 1994). Wolverines lead a solitary lifestyle, occupying large home ranges at low population densities in areas remote from humans and human developments (Banci 1994). All three factors have combined to make research studies difficult and therefore infrequent.

North American field studies completed in the 1980s included two in Alaska (Gardner 1985; Magoun 1985), one in the Yukon (Banci 1987) and one in Montana (Hornocker and Hash 1981). An additional study completed in 1996 in central Idaho (Copeland 1996) added to our knowledge of wolverine presence, ecology, spatial characteristics, movement, demographics, social structure and habitat use.

The most common attributes derived from field studies of wolverine are large spatial requirements, low population density, and nonspecific habitat requirements in terms of vegetative structure (Copeland 1996). Hornocker and Hash (1981) described a wolverine population in northwest Montana as demographically stable, but socially dynamic due to periodic turnover caused by trapping mortality. Their research was the only field study of wolverines in the contiguous U.S. before Copeland (1996). Gardner (1985) studied wolverines in south-central Alaska and concluded that the Alaskan population was more spatially stable than the Montana population. Magoun (1985) included behavior in her assessment of factors important to management of an arctic Alaska wolverine population dependent on migrating ungulates. Banci (1987) analyzed wolverine carcasses to determine reproductive morphology and food habits and studied wolverine ecology and habitat use in the Yukon.

A main theme that has emerged from past research on wolverines is that information necessary for the management and conservation of wolverine populations in Western forests is not available (Banci 1994). 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 (Banci 1994).

Results from research conducted in central Idaho include recording the largest spatial requirements for wolverine, with male home ranges averaging 1,522 km^2 and female home ranges averaging 384 km^2 (Copeland 1996). In addition to documentation of spatial requirements, Copeland (1996) described evidence of a resident adult wolverine associating with a sub-adult wolverine, behavior not previously recorded. Research results reported from this study were an outcome of advances in biotelemetry, enabling researchers to study wolverine ecology in a more comprehensive manner.

Survey methods to detect the presence of wolverines have also benefited as a result of new technology. William Zielinski, research wildlife biologist with the Pacific Southwest Research Station, and Thomas E. Kucera, of the Department of Environmental Science, Policy, and Management, University of California-Berkeley, have produced a document detailing successful methods used to detect the presence of forest carnivores, including wolverines. The survey methods

described in the manual produce necessary, reliable and verifiable information on the distribution of wolverines (Zielinski and Kucera 1995). Detection methods described in the manual include remote camera, track plate and snow-tracking methods.

Wolverine field studies confirm a clear association between wolverine presence and refugia. Hatler (1989) commented that reduction of wilderness "refugia" through access and alienation for timber and mineral extraction may be the greatest threat to local population viability. Banci (1994) confirms that persistence of a population of wolverine in southwestern Alberta is due to the presence of large refugia, in the form of national parks.

The absence of wolverines from historical ranges may be related to human activity as much as reductions in habitat (Copeland 1996). Reduction in the wolverine's historical North American distribution and numbers is suspected to be a result of human encroachment (Banci 1994). Human presence within historical wolverine range may have regulated population growth and stability or simply displaced wolverines through habitat alteration and destruction (Copeland 1996). 'Female wolverines used secluded high-elevation cirque basins in Idaho for natal den sites. Protection of natal denning habitat from human disturbance is critical for the persistence of wolverine in Idaho (Copeland 1996). Human disturbance at maternal dens resulted in den abandonment, but not kit abandonment The advent of increased use of wilderness areas by snowmobilers and other winter recreationists in the 1990s is believed to have displaced wolverines from potential denning habitat.

Limited information, indicates that wolverines appear more susceptible to natural fluctuations in scavenging opportunities and may have lower lifetime productivity than even grizzly bears (Weaver and others 1996). The reproductive rate for females was less than 1 kit/female/year (Copeland 1996).

Increased public awareness of the habitat requirements of wolverines and the role they play in the functioning of wilderness ecosystems will be key in their conservation. Wolverines' current listing as "sensitive" or as a "management indicator species" on most national forests throughout their range should provide increased levels of administrative and legal protection (Zielinski and Gill 1997).

New research initiatives and the accompanying results will help provide forest managers with the information needed to determine the ecosystem components necessary to sustain wolverine populations. Planning for species conservation can be less difficult and more beneficial than trying to restore declining populations.

Wolverines thus constitute a classic wilderness-dependent species. They require large spatial areas with a full array of seasonal habitats to maintain their solitary lifestyle, as well as the necessary refugia from human influences. Ideally, such wilderness refugia should be connected to other refugia through landscape linkages (Weaver and others 1996). 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 a high research priority (Bianci 1994).

Wilderness Research and Mountain Lions

Mountain lions have adapted to - and been studied in - a wide range of habitats in North America. However, wilderness areas have provided unique research opportunities to study natural regulation, mountain lion social systems, home ranges and habitat use.

The study of natural regulation is important to wilderness wildlife researchers because results of research studies have broad implications for management of big game. Natural regulation, by definition, can take place only in ecosystems where predator, prey and habitat are not impacted by human activity. Predator-prey relationships constitute one form of natural regulation that can be defined as the set of controlling mechanisms that serves to limit population density in the absence of human influence (Peek 1980). Ideally, this research is conducted in a wilderness setting that includes the opportunity to encompass all phases of population fluctuation of mountain lions and their ungulate prey.

Hornocker (1970) began an investigation to gather information on mountain lion population dynamics and to assess the lion's role as a predator in the Idaho Primitive Area (now the Frank Church River of No Return Wilderness). Hornocker primarily used mark-release-recapture techniques, with tracking dogs and snow tracking, to locate the mountain lions. He discovered that in spite of both lion and human predation, populations of mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*), increased during a four-year period during which the lion population remained stable. Hornocker (1970) postulated that, "Intraspecific relationships, manifested through territoriality, acted to limit numbers of lions and maintain population stability. Dispersal and mortality of young individuals appeared to be an important limiting mechanism."

Radio-tracking, developed successfully by Craighead and Craighead (1972) and used for tracking grizzly bears, was implemented in subsequent mountain lion research in the Idaho Primitive Area by Seidensticker and others (1972). The use of biotelemetry enabled the researchers to observe the highly secretive mountain lion and describe its social system. Seidensticker and others (1972:77) concluded, "that the lion land tenure maintains the density of breeding adults below a level set by food supply in terms of absolute numbers of mule deer and elk. Variation in mountain lion environmental structure resulted in variations in the suitability of areas and affected the amount of terrain a resident lion utilized. The amount of terrain used by a resident mountain lion as well as the degree of home area overlap between resident females, i.e., density of breeding population, was set by a vegetation-topography/prey numbers-vulnerability complex."

These early mountain lion research studies identified the social system and intrinsic regulatory mechanisms involving territoriality and land tenure, which provides baseline information needed to manage and conserve this species and other solitary cats (Hornocker and Bailey 1986). They were possible because of the extent of the large wilderness areas in central Idaho. It was through this work that the mountain

lion was designated a game animal in Idaho (Hornocker 1971). Subsequently, this species was designated a game animal in most states and provinces that maintain populations, and an orderly regulated harvest was then established (Peek 1999).

Sweanor (1990) expanded the research completed by Seidensticker and others (1972) by completing a comprehensive study of mountain lion social behavior in a desert environment. In this study, Sweanor (1990) concluded that mountain lion populations in the San Andres Mountains of New Mexico appear to be self-regulating. Self-regulation probably is imposed via three mechanisms: social intolerance, mortality from intraspecific killing and dispersal.

Research studies have employed intensive search, capture, marking, recapture and radiotelemetry techniques and defined analytical methods. The research studies areas include Alberta (Ross and Jalkotzy 1992), British Colombia (Spreadbury 1989), Idaho (Seidensticker and others 1972), New Mexico (Logan and others 1996), Utah (Lindzey and others 1994) and Wyoming (Logan and others 1986). These studies produced the most reliable estimates of mountain lion density. Maximum densities reached 0.6 to 2.2 resident adults or 1.4 to 4.7 mountain lions per 100 square kilometers (Logan and Sweanor 1999).

Important findings from the past 25 years of mountain lion research include these results (Logan and Sweanor 1999):

1. Deer are mountain lions most important food, although other species of ungulates are eaten depending on local abundance and vulnerability (Anderson 1983).
2. Mountain lions can be cannibalistic. Males have killed and cannibalized cubs (Hemker and others 1982; Logan and others 1996; Spreadbury and others 1996; Young 1946), adult females (Beier and Barrett 1993) and other adult males (Williams 1992).
3. How often that mountain lions kill prey and their rates of consumption largely depend on the energy requirements of the individual population units and the biomass of the prey (Logan and Sweanor 1999).
4. Mountain lions are polygamous and promiscuous (Anderson 1983; Seidensticker and others 1973; Sweanor 1990).
5. The social organization of mountain lions has been described as a land tenure system where dominance over an area is held initially by the resident adult mountain lions occupying the area (Seidensticker and others 1973).
6. Home ranges of mountain lions have been studied extensively using radiotelemetry; in general, home ranges of males are larger than females within the same population by factors of 1.5 to 5.

Gaps in information concerning mountain lion ecology include little information on the age structure of mountain lion populations, data on sex and age-specific survival rates, the effects of parasites and disease in mountain lions and quantitative information on rates of mountain lion population increase (Logan and Sweanor 1999).

Wilderness areas are important to mountain lion research and conservation for several reasons including: (1) the potential to provide a diversity of genotypes when selection outside of wilderness areas is heavily influenced by humans, (2) the potential to conduct long-term research, spanning more than 10 years, to determine to what extent mountain lion predation limits or regulates prey populations (Logan and Sweanor 1999) and (3) knowledge of how mountain lions use habitat in an unaltered landscape which should help managers identify potential degradation and fragmentation, locations of migration and dispersal corridors.

Protected mountain lion populations, particularly in national park wilderness areas function as robust biological savings accounts which contribute to population resilience (Weaver and others 1996) by countering management-related mistakes in exploited subpopulations and increased mortality in adjacent fragmented habitat (Logan and others 1996; Murphy 1998). Protected areas enable subpopulations to evolve relatively naturally, providing a diversity of genotypes when selection is heavily influenced by humans (Logan and others 1996).

Long-term (greater than 10 years) experimental research will be needed to determine to what extent mountain lion predation limits or regulates prey populations. Murphy (1998) states, "I am unaware of a single study of cougar population dynamics that has spanned even one full cycle of major fluctuation in its principal prey." Studies have not been long enough to include all the phases of fluctuation of a population of the mountain lion and its ungulate prey.

Knowing how mountain lions use habitat in wilderness areas should help land managers identify potential degradation and fragmentation and locations of dispersal and migration corridors. Habitat loss and fragmentation are the greatest threats to long-term mountain lion conservation (Logan and others 1996).

Wilderness Research and Grizzly Bears

The nature of the grizzly bear as an animal that requires significant amounts of space, solitude from excessive human disturbance and a broad range of diverse and available habitats makes it a prime example of a wilderness animal (Servheen 1985). Space and solitude are essential for maintaining bears in perpetuity, therefore research and management efforts should focus on the largest areas of prime bear habitat (Craighead and others 1982).

Evidence of a decline of grizzlies in Yellowstone, combined with aroused public concern over the fate of this powerful carnivore in the contiguous 48 states, prompted the director of the U.S. Fish and Wildlife Service, following scientific and public review, to declare the grizzly bear a threatened species subject to the rules and regulations of the Endangered Species Act of 1973 (Craighead and others 1982). This designation emphasized the importance of critically defining and analyzing components of grizzly bear habitat and relating this information to the numbers and distribution of the bears (Craighead and others 1982).

The grizzly has survived through the past decade primarily because suitable habitat was preserved by the Wilderness Act of 1964, which established a National Wilderness Preservation System. The focus of research on grizzly bears, from the 1970s to the 1990s, has been on describing, analyzing and mapping critical wilderness habitat occupied by bears.

Critical habitat was delimited and land areas classified that are: (1) in wilderness status and currently supporting viable grizzly bear populations; (2) occupied by grizzly bears, but subject to high priority land use conflicts; and (3) wilderness or *de facto* wilderness no longer supporting viable grizzly bear populations, but having the habitat potential to do so (Craighead and others 1982). Craighead and others (1982) suggested that researchers use these broad habitat classifications as a starting point for intensive study and scientifically describing the areas delineated.

Many habitat studies have been completed on various aspects of grizzly bear habitat south of Canada, including habitat surveys, establishment of criteria for evaluating habitat, development of habitat rating systems, development of habitat-typing and mapping techniques, analyses of food plant distribution and occurrence and food habits of grizzly bears in relation to habitat types and generalized vegetation complexes. Craighead and others (1982) utilized satellite multispectral imagery and ecological ground truth data to construct thematic, computerized vegetation type maps. Studies of the food habits and habitat requirements of grizzly bears, in wilderness areas, has revealed that environmental characteristics essential to the maintenance of a grizzly bear population include (Craighead and others 1982):

1) Space – large wilderness areas of national parks and national forests are essential. Home ranges encompass an area up to 2,600 to 4,000 sq. km.

2) Isolation – Habitat must be isolated from developed areas and conflicts with man.

3) Sanitation – Disposal of garbage at communities adjacent to essential habitat to eliminate bear-man conflicts.

4) Food – Abundance of natural foods must be available from April to November.

5) Denning – Wilderness areas that provide the specific denning requirements (2,100-2,750 m altitude in areas of heavy snowfall) and isolation during the denning period.

6) Vegetation Types – Wide range of vegetation types.

7) Safety – Protection from human depredation and competitive use of habitat.

A perceived threat to wilderness areas, which has influenced current trends in grizzly bear research, is a result of the scientific use of wilderness (Franklin 1987, Parsons and Graber 1990). Research in wilderness areas often requires the use of permanent markers, mechanized equipment and/or destructive sampling. The trend in the past 20 years or so, since the advent of radiotelemetry, has been to capture and radio-collar grizzly bears in wilderness areas to obtain population parameters. There is evidence that an intensive trapping program that subjects an already stressed population to a high degree of disruption and human-conditioning is highly questionable and not biologically or financially justifiable (Craighead and others 1982).

In 1985, the development of a population monitoring system was identified as a high priority item in the Grizzly Bear Recovery Plan for the northern Continental Divide ecosystem. There is need to assess population change over time without jeopardizing the population by subjecting bears to capture and placement of radio collars. Identified design criteria that must be met by any trend monitoring system include: 1) it should be cost-effective; 2) it must measure a representative sample of an acceptable size; 3) it must not cause more than minimal disturbance to the bears and the ecosystem; and 4) it must be easy to use (Eno and others 1986).

In the northern Continental Divide ecosystem, several methods to assess population trends were tested from 1982 to 1984. These included helicopter surveys of known denning areas when bears emerged in the spring, helicopter surveys of shrub fields in autumn when the shrub fruit crop was at its peak, and aerial and ground surveys of open alpine areas in summer (Eno and others 1986).

New advances in genetic technology allow identification of species, sex and individuals from DNA extracted from bear hair and scats without handling bears (Waits, unpublished). These new techniques are less expensive and less disruptive to bears than traditional censuses using radiotelemetry and radio-tracking. Hair samples are collected at bait stations, and bear sign is collected along trails frequented by bears. This information should enable researchers to document ecosystem-wide population trends. Research is now being conducted at Glacier National Park using genetic technology.

Wolves and Wilderness Research

Wolf research in a wilderness setting began as early as 1958 in Isle Royale National Park (Mech 1966). Researchers were interested primarily in understanding the factors that regulated wolf and moose (*Alces alces*) populations on the island. Isle Royale National Park provided the perfect opportunity for this type of study as the wildlife populations were confined to this isolated island, with no real possibilities for emigration or immigration. In terms of faunal diversity, the island is also a relatively simple system. A number of bird and mammal species that exist on the mainland have never reached the island or have since disappeared from it. The community of life on the island is therefore easier to work with and understand than similar habitats in Minnesota and Ontario (Allen 1993).

Another important advantage is that no hunting or trapping is allowed on the island. If Isle Royale had been hunted, the age structure of the moose herd would have been altered, and many moose would have been shot long before they were old enough to be killed by the wolf (Allen 1993). If beaver had been subject to trapping, the summer food supply of wolves would have been reduced. If wolves had been exposed to control or illegal shooting, the social relationship of individuals and packs would have been disrupted. Finally, the Park is closed to visitor-use during the winter, and visitor activities during the summer are relatively nonintrusive and closely monitored (Wright 1996).

The research program at Isle Royale National Park has concentrated on three main topics over the years: wolf predation patterns, wolf behavior and ecology and moose population dynamics. Studies of wolf predation patterns emphasized the age and sex of moose killed, the other prey species, hunting success and the effect of snow depth on predation success and activities. Research on wolf behavior and ecology focused on social hierarchy in the packs, courtship and breeding, territoriality, communication, denning and rendezvous sites, reproduction, relationships with non-prey species and movements. Field observations of moose population dynamics included population size, age and sex

ratios and productivity, habitat relationships, food habits and mortality factors (Wright 1996).

Important insights into predator-prey relationships have been gained in the almost 40 years of wilderness research at Isle Royale National Park, but not without controversy. Evidence of stable limit cycles at Isle Royale was presented by Peterson and others (1984) and reconfirmed by Messier (1991). Stable limit cycles imply density-independent predation during increases in moose density, inversely density-dependent predation during moose declines, regular periods of oscillation, no predator pits and nonregulating predation throughout the cycle (Van Ballenberghe and Ballard 1994).

Keith (1983) proposed recurrent fluctuations as a general model for moose-wolf interactions when bears were absent, and Van Ballenberghe (1987) interpreted the Isle Royale data as evidence of this, in contrast to stable-limit cycles. Recurrent fluctuations occur if predation is mainly density-independent or inversely density-dependent and not regulating. Van Ballenberghe and Ballard (1994) reviewed the recent literature on moose-predator interactions to determine whether moose numbers are limited or regulated by predation, and if so, under what conditions. The authors conclude that "the conditions required for recurrent fluctuations include minimal influence by humans on simple moose-wolf ecosystems containing few alternative prey. The Isle Royale data from 1959 to 1969 represent periods of increase (1959-1969), decrease (1970-1980) and increase (1981-1986) (Messier 1991) that fit the recurrent fluctuation model." They further state that, "Because Isle Royale is a unique example of a moose-predator system lacking bears, it may be the best area to test the recurrent fluctuation model for naturally regulated ecosystems."

The central tenet of natural regulation envisioned by Cole (1971) and D. B. Houston, (unpublished manuscript)—that moose exhibit intrinsic demographic responses sufficient to stabilize population growth—was not supported by a chronological review of moose fluctuations at Isle Royale completed by Peterson (1999). Depressed wolf numbers led to an increase in moose which continued until moose overshot their food supply and crashed from starvation.

Houston (1982) stressed that the lack of wolf predation for the majority of this century in most national parks was a significant ecological deficiency (Peterson 1999). Wilderness research opportunities for studying wolves in recent years have involved monitoring efforts and documenting the restoration of large carnivores in wilderness areas. The restoration of wolves to Yellowstone National Park and the Middle Fork of the Salmon River, Idaho in 1995 have enhanced the value of these areas as ecological research sites (Phillips and Smith 1996) and provided wilderness researchers with a unique opportunity. Peek (1999) states that, "As wolves continue to adjust to this area, opportunities to investigate their interactions with other predators, most especially the mountain lion which shares a common prey base, and to examine the effects on prey that are game species are obviously great." An investigation into the relationships of four carnivores—mountain lions, wolves, coyotes and bobcats—was initiated in December 1998 in the Big Creek drainage in central Idaho.

The major need in future research is to understand the role of wolf predation in regulating ungulate prey (Eno and others 1986). Wolves and their prey are long-lived (Peterson and others 1984), and unraveling predator-prey dynamics requires a long-term research commitment. Long-term studies often show that systems, even those considered to be relatively simple, are in fact very complex. Over the course of the Isle Royale research, different perspectives of what is going on emerged at different points in the time period. It seems clear that if the research had been terminated at any one of these points, our biological understanding of the system would be far different and probably flawed (Wright 1999).

Lynx and Wilderness Research

The lynx occurs primarily in the boreal forests of Alaska and Canada, but its range extends south into the northern portion of the Western mountains, where environmental conditions at high elevations support boreal forest habitats similar to those found in northern regions. The distribution of the lynx appears to be tied to that of the snowshoe hare (*Lepus americana*), and both species are confined to northern forest environments (Hall 1981). Snowshoe hares comprise 35%-97% of the lynx diet (Koehler and Aubry 1994). Hares not only determine where lynx are found, but also influence how many lynx may occupy an area.

The conservation of lynx is of greatest concern in the Western mountains of the conterminous United States at the southern periphery of the species' range (Koehler and Aubry 1994). The largest populations in the United States, outside of Alaska, occur in the northern portions of Washington and Montana. A current description of lynx distribution in Washington indicates that lynx are now restricted to the northeastern Cascade Range and several isolated areas in the Okanogan Highlands of northeastern Washington (Koehler and Aubry 1994). The Okanogan population was studied with radiotelemetry in the 1980s (Brittell and others 1989; Koehler 1990), and most of the information available on the ecology, population dynamics and management of the lynx in the Western mountains of the United States comes from these studies. Historical records indicate that lynx were relatively numerous in the panhandle of Idaho and western Montana.

Recent lynx records are scarce from the Western mountains and reliable information on the current distribution and abundance of lynx populations throughout the western United States is needed (Koehler and Aubry 1994). Only five lynx studies have ever been conducted in the Western mountains of the United States, including two in Washington and three in Montana. These studies have focused on home range and habitat use; information on demography, food habits, dispersal and denning sites is lacking. Koehler and Aubry (1994) state that studies on foraging ecology, den site characteristics and habitat relationships at the landscape scale are urgently needed.

Conclusions

Wilderness is vital to the conservation of wildlife species prone to conflict with humans as well as to species that require wilderness to provide an array of seasonal habitats necessary for survival. Research in wilderness areas is not necessary or practical for the majority of wildlife species

because these animals do not fit the requirements for wilderness-dependent wildlife.

Wilderness wildlife researchers must remind themselves that it is not so much the nature of wilderness that demands the efforts of researchers, but the animals that exist only in wilderness areas. Mountain lion research can be accomplished outside of wilderness areas because mountain lions exist in a variety of habitats. Grizzly bear, wolf, lynx and wolverine research can only occur in wilderness areas because these are the only habitats where these animals can be found in sufficient numbers.

One facet of research that depends on wilderness areas, especially those in national parks, is the study of natural regulation. The study of natural regulation can only take place in wilderness settings where predator, prey and habitat are not impacted by uncontrolled human activity and human harvest. This may rule out wilderness settings subject to a high level of hunter harvest.

The presence of large areas with a high degree of integrity and continuity means that a wilderness harbors substantial information of benefit to science and society (Graber 1985; Noss 1991). However, wilderness wildlife research has been primarily limited to species that are wilderness-dependent and the study of natural regulation. Many more wildlife research questions can be answered outside of wilderness areas more easily and at less cost. Perhaps the focus on wilderness research should be on ecological processes rather than specific wildlife species, unless we are trying to unravel specific survival questions pertaining to wilderness-dependent wildlife or studying natural regulation.

We conclude by stating that wilderness is important to the conservation of wilderness-dependent species, but conclusions drawn from analyses of the published literature indicate that wilderness and wildlife research is limited in scope on the majority of wildlife species. This trend will no doubt continue due to limited funding and accessibility. There may be no scientific basis for studying a population of mule deer in a wilderness area, as opposed to a population in a habitat adjacent to a populated area, unless the basis for the research is to assess the impacts of human-caused mortality or the study of natural regulation.

Although wilderness wildlife research, for all practical purposes, is limited to the study of wilderness-dependent wildlife and natural regulation, researchers should be aware of and make greater use of the opportunities to monitor wildlife populations in wilderness settings. Monitoring wildlife in wilderness ecosystems may be used to warn of impending environmental change across broad geographic areas. Davis and Halvorson (1988) considered the national park ecosystems to be "miner's canaries" and the concept applies to many areas that are relatively undisturbed by human presence (Peek 1999).

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