

INTEGRATION OF ENVIRONMENTAL, BIOLOGICAL, AND HUMAN
DIMENSIONS FOR MANAGEMENT OF MOUNTAIN LIONS
(*PUMA CONCOLOR*) IN MONTANA

A Dissertation

Presented to the Faculty of the Graduate School
of Cornell University

in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

by

Shawn James Riley

August 1998

© 1998 Shawn James Riley

INTEGRATION OF ENVIRONMENTAL, BIOLOGICAL, AND
HUMAN DIMENSIONS FOR MANAGEMENT OF MOUNTAIN LIONS
(*PUMA CONCOLOR*) IN MONTANA

Shawn James Riley, Ph.D.

Cornell University 1998

Recent increases in mountain lion (*Puma concolor*) populations throughout western North America challenge wildlife managers who attempt to achieve a balance between the beneficial and detrimental aspects of a large carnivore in human dominated environments. A lack of understanding of the environmental, biological, and human dimensions that affect mountain lions and the interrelationships of these dimensions has been an impediment to effective lion management. I used a combination of ecological and social science methods to determine: (1) factors that influence the distribution and abundance of mountain lions; (2) vital rates that most affect lion population growth; and, (3) factors that determine stakeholder preferences for lion populations. Records of 4,057 mountain lion deaths from 1971-1994 were used to develop a total mortality index (TMI) as an indirect index of mountain lion abundance. A 2-factor model that included quantitative measures of lion habitat and white-tailed deer (*Odocoileus virginianus*) abundance was the most parsimonious model ($r^2 = 0.78$) for prediction of TMI on a state-wide basis. Within specific ecoregions, there was a strong linear relationship ($r^2 = 0.89$) between white-tailed deer abundance and TMI in the Montane Ecoregion west

of the continental divide. A similar strong linear relationship ($r^2 = 0.74$) existed between elk

(*Cervus elaphus*) abundance and TMI in the Intermountain Ecoregion of southwest and central Montana. Sensitivity analyses of a stochastic population simulation model indicated adult survival was the most important vital rate in affecting the intrinsic rate of increase in lion populations. A mail questionnaire was used to determine factors that affect stakeholder preferences for mountain lion populations. A 3-factor model that included measures of respondent's perceptions about the direction of current mountain lion population trends, attitudes towards lions, and beliefs about risks to humans from lions, correctly predicted the desired trend of 73.8% of respondents who wanted a smaller lion population and 90.8% who wanted a larger population or no change. Recommendations to influence the environmental, biological, and human dimensions of mountain lions are presented within integrated management matrices. Implications of the temporal and spatial scales and the interrelationship of the 3 management dimensions are discussed.

“The panther is found indifferently either in the Great Plains of the Columbia, the western side of the Rocky Mountains or the coast in the timbered country. It is precisely the same animal common to our Atlantic coast, and most commonly met on our frontiers or unsettled parts of the country. This animal is scarce in the country where it exists and are so remarkably shy and watchful that it is extremely difficult to kill them.”

William Clark
 Thursday, February 27, 1806
 Fort Clatsop, Columbia River
The Journals of Lewis and Clark

“We can’t have panthers running around in a country where there are little girls.”

Pa Ingalls
Little House on the Prairie
 Laura Ingalls Wilder (1935)

“These animals are so destructive to man’s interests that they can not be tolerated except in the wildest areas.”

Young and Goldman (1946)
The puma: Mysterious American Cat

“Controls we may need, what is called game-management we may need, for we have engrossed the earth and must now play God to the other species. But deliberate war on any species, especially species of such evolved beauty and precise function, diminishes, endangers, and brutalizes us. If we cannot live in harmony with other forms of life, if we cannot control our hostility toward the earth and its creatures, how shall we ever learn to control our hostility toward each other?”

Wallace Stegner (*in* McCall and Dutcher 1992)
Cougar: Ghost of the Rockies

“What we learn from the lion and the mule deer is more about what we believed than what we know.”

Daniel Botkin (1990)
 Discordant Harmonies

ACKNOWLEDGMENTS

I am indebted forever to my entire family, but especially my wife Shari, who encouraged me to pursue my dreams and allowed me to occasionally stray off-course in the spirit of a liberal doctoral experience. Shari, Aaron, and Kristen helped me keep perspective on what is most important while on a journey such as the one we have traveled together these past five years.

My graduate committee provided a multitude of services, support, and time for which I am sincerely grateful. Richard A. Malecki advised, supported, patiently read, and enthusiastically cheered me on through completion of the project. Daniel J. Decker provided excellent, concise advice and timely, quality critiques at critical moments. William Schulze introduced me to the topic of risk analysis and its economic implications while providing valuable philosophical discussion along the way. Milo E. Richmond stayed with me from the beginning, provided sound advice, and kept us all honest with cogent questions and suggestions. Many thanks to Bruce T. Wilkins, my initial advisor, for bringing me to Cornell and for advice during the initial phases of my dissertation project.

As with any collaborative project, my research would not have been possible without a great many people. In Montana, Glenn Erickson and John McCarthy facilitated agency support and advice throughout the project. Keith Aune shared his computer files of lion mortality data. Candy Haskins and Steve Martin facilitated retrieval of ungulate harvest data and generated lists of hunting license holders. Dana Dolsen facilitated administration of the mail questionnaire and subsequent data entry. Every biologist I worked with in

Montana, too many to list without leaving some out, gave me timely help and advice when I needed it. Many provided food and cover as well.

Members of the Human Dimensions Research Unit patiently provided guidance and criticism on numerous occasions as this wildlife biologist ventured into the social science arena. Heidi Cristoffel was especially helpful with telephone non-response surveys and analyses that required SPSS, while Nancy Connelly provided gentle guidance on appropriate statistical procedures. Nancy Connelly, Jody Enck, and Bruce Lauber provided critiques that improved the mail questionnaire. Tommy Brown consulted on sampling techniques and sample sizes. Barbara Knuth provided thoughtful suggestions about inquiries into risk perception, and was very helpful in many other aspects of professional development along the way.

Susan Sheaffer provided statistical consulting at numerous points in the planning and analysis. Many graduate students provided helpful critiques and discussion during my research, including but certainly not limited to: Scott Boomer, Lisa Chase, Jody Enck, Caleb Kleppner, Bruce Lauber, Michael Runge, Roland Shanks, Jim Tantillo, and Josh Winchell. Several undergraduate students conducted independent projects that helped with my data analyses. Sean Burrows helped various aspects of computer support and conducted a spatial analysis of mountain lion-human conflicts. Barbara Cliff helped compile and analyze bounty data. Rob Elliott helped construct the terrain ruggedness index model and made initial GIS ruggedness coverages. A heartfelt thanks to all.

My research was financially supported by the following organizations (listed alphabetically): Boone and Crockett Club, Cinnabar Foundation, Cornell University, Montana Chapter of Safari Club International, Montana

Fish, Wildlife and Parks, Pope and Young Club, Sea Grant, and US Department of Agriculture Forest Service Intermountain Research Laboratory -- Missoula, and the US Geological Survey Biological Resources Division. In addition, I was generously supported by a Clinton Dewitt Fellowship in Life Sciences and 2 Gifford Pinchott Fellowships in Conservation.

TABLE OF CONTENTS

		Page
	List of tables	x
	List of figures	xi
I	Introduction	1
II	Study area	6
III	Factors affecting the distribution and abundance of mountain lions (<i>Puma concolor</i>) in Montana	12
	Literature review	14
	Methods	19
	Results	23
	Discussion	30
IV	Sensitivity analysis of a stochastic population simulation model for mountain lions (<i>Puma concolor</i>): implications for management	35
	Literature review	37
	Methods	44
	Results	49
	Discussion	54
	Management implications	58
V	Factors that affect stakeholder preferences for mountain lion (<i>Puma concolor</i>) populations in Montana	60
	Literature review	63
	Methods	68
	Results	72
	Discussion	93

	Page
Management implications	98
VI Integration of environmental, biological, and human dimensions for management of mountain lions (<i>Puma concolor</i>)	103
Appendix I Research needs for mountain lions in Montana	115
Appendix II An analysis of the number of mountain lions and wolves killed during the bounty system in Montana, 1887 -1962	118
Appendix III The model used to formulate a terrain ruggedness index (TRI) using ARC/INFO geographical information system	126
Appendix IV A self-administered mail questionnaire used for inquiry into the beliefs, attitudes, risk perception, and mountain lion population preferences of stakeholders in Montana, 1997	130
VIII Literature cited	142

LIST OF TABLES

	Page
3.1 Table 3.1. Regression coefficients that describe the relationship between mountain lion and ungulate indices of abundance in Montana, 1976-1994. P-values shown in parentheses	26
4.1 Population characteristics of mountain lions from selected studies areas in North America	47
5.1 Percent of questionnaire respondents from west, central, and eastern Montana that indicated they participated in various outdoor activities	75
5.2 Percent of questionnaire respondents from west, central, and eastern Montana that indicated they had various involvement with mountain lions	76
5.3 Correlation coefficients of key variables in the model to predict preferences for future mountain lion populations in Montana	80
5.4 Response of Montanans to belief statements used in the scale to form the variable ATTITUDE regarding mountain lions in Montana	85
5.5 Response of Montanans to semantic differential items related to risks from mountain lions to human safety in Montana, 1997	86
AII.1 The total wolf and mountain lion bounty payments by Montana counties, 1900-1931	121

AII.2 The total wolf and mountain lion bounty payments, 1900 - 1931, adjusted for 1900 Mountain counties	123
AIII.1 Terrain ruggedness index (TRI) values for 1995 hunting districts (HD) in Montana	128

LIST OF FIGURES

	Page
2.1 The physiography of Montana with county boundaries included. The map was derived from a USGS 1 km. digital elevation model (http://nris.mt.gov/nsdi/nris/e00)	7
3.1 Mountain lion mortality in the Montane, Intermountain, and Prairie Ecoregions of Montana, 1971 - 1994	24
3.2 The relationship between HABITAT and the total mortality index of mountain lions in Montana. HABITAT was the product of a terrain ruggedness index and the proportion of a hunting district in forested habitat types	25
3.3 The relationship between the statewide total mortality index for mountain lions in Montana and (a) white-tailed deer buck harvest, (b) mule deer buck harvest, and (c) elk harvest. Data are for mountain lion hunting districts	27
3.4 The relationship between the total mortality index for mountain lions and density of buck white-tailed deer harvest in the Montane Ecoregion of Montana, 1978- 1994. Data are for mountain lion hunting districts	29
3.5 The relationship between the total mortality index for mountain lions and density of total elk harvest in the Intermountain Ecoregion of Montana, 1978- 1994. Data are for mountain lion hunting districts	29

4.1	The annual life cycle of mountain lions in Montana as depicted in a stochastic birth and death population simulation model	46
4.2	The distribution and range of the finite rate of increase (λ) for mountain lions based upon 1,000 replicates of a stage-structured population model. Values for stage-specific survival rates, litter size, and age of first reproduction within bounds established from field studies (Table 4.1)	50
4.3	Regression analyses of vital rates on the finite rate of increase for mountain lions based upon 1,000 replicates of a stage-structured population model. Vital rates were randomly selected from a uniform distribution within bounds established from field studies (Table 4.1)	51
5.1	Percent of respondents from western, central, and eastern Montana that indicated their interest and participation in wildlife-related activities	73
5.2	Percent of questionnaire respondents from west, central, and eastern Montana with various levels of involvement with mountain lions	77
5.3	The proportion of respondents from western, central, and eastern Montana that expressed preferences for a smaller, no change, or larger mountain lion population in their area of the state	78

5.4	The proportion of respondents from western, central, and eastern Montana that believed the mountain lion population in their areas either decreased, did not change, or increased during 1991-1996	81
5.5	The proportion of respondents with various levels of involvement with mountain lions in Montana that indicated a decreased, no change, or increased mountain lion population in their areas during 1991-1996	82
5.6	The proportion of respondents from western, central, and eastern Montana that expressed different feelings toward mountain lions	83
5.7	The distribution of perceived societal risk to human safety from mountain lions relative to more common risks	88
5.8	A comparison of subjective risk judgments of respondents that desire a (a) decreased, (b) no change, and (c) increased mountain lion population	89
5.9	A comparison of perceived risks to human health and safety from mountain lions in Montana, by level of involvement with mountain lions. (A) low, (b) medium, (c) high, (d) very high	91
5.10	A cost:benefit display of the costs associated with different estimates of perceived risk to humans from mountain lions	96
6.1	The spectrum of implicit decision/effects of the human, environmental, and biological dimensions associated with wildlife management	105

	Page
6.2 The space of implicit decision/effects associated with mountain lion management. (a) subdivision development, (b) hunting regulations, and (c) predator-prey interactions	106
6.3 Spatial and temporal scales associated with different dimensions of mountain lion management (Adapted from Litvaitis et al. 1996)	107
6.4 An integrated mountain lion management matrix that depicts potential management situations under various population levels and population management directives	110
AII.1 Montana county boundaries used for collection of bounty payments on mountain lions and wolves (Thorndale and Dollarhide 1987)	119
AII.2 Number of mountain lion and wolf hides presented for bounty payment in Montana, 1884 - 1931	120
AII.3 A comparison of the cumulative density of wolf and mountain lion bounty payments, 1900 - 1931, by ecoregion in Montana	125
AIII.1 A grid diagram that depicts the model from which a terrain ruggedness index was calculated	126

CHAPTER ONE

INTRODUCTION

Mountain lions (*Puma concolor*) present a unique challenge in wildlife conservation for nearly every western state and province. Considered rare 30 years ago, mountain lions in western North America are now 1 of only 2 large (i.e. mean adult weight > 20 kg) felid species to increase their distribution and abundance coincidental with increased human development. African leopards (*Panthera pardus*) are the only other large felid that has flourished in recent years (Nowell and Jackson 1996). Mountain lions were eradicated in most of North America by 1930 (Young and Goldman 1946). However, mountain lions increased their distribution and abundance throughout the West since World War II (Padley 1997:97-124), and are reported now in areas where they were historically rare or absent (Nero and Wrigley 1977, Berger and Wehausen 1991). Recent confirmation of mountain lions in the Great Plains states implies an eastward expansion of their distribution (Genoways and Freeman 1996). During the time lions have been increasing, the American West also experienced the most massive redistribution of human populations since early land-rush days of the late 1800's (Riebsame 1997:95). Eight of the 10 states with the fastest growing human populations during the 1990s are west of the Great Plains and support populations of mountain lions.

Increases in human and mountain lion populations have created new dilemmas for people living, working, and recreating in the West, as well as for wildlife agencies who lack needed information to manage mountain lions in this changing environment (Olsen 1992). Research on mountain lion ecology before 1980 was confined to a few studies in a single Idaho study area

(Hornocker et al. 1970, Seidensticker et al. 1973). Those reports, which then formed a basis for much of the mountain lion management during 1970 - 1990, suggested lions were a wilderness species that occurred in relatively low densities. A low density of mountain lions was hypothesized to be maintained through a form of territoriality called land tenure (Seidensticker et al. 1973).

Wildlife managers were unprepared for an apparent surge in mountain lion populations that occurred in the late 1980s and continued into the 1990s (Olsen 1992, Padley 1997). Mountain lion attacks since 1988 in British Columbia, California, Colorado, Montana, and Washington caused at least 7 human fatalities and numerous injuries (Beier 1991, Stevens 1994). An increase in mountain lion “incidents” in Montana created unanticipated, but significant changes within that state’s wildlife agency. For example, game wardens in Montana responded to 108 mountain lion-human incidents during 1994 just in the vicinities of Kalispell and Missoula (Warden Captain E. Kelly, pers. comm. 2/21/95). Those management responses resulted in at least 13 mountain lions killed, and considerable attention from the press. Other western states reported similar situations (Braun 1992, Padley 1997).

Increased frequency of mountain lion-human incidents raises questions of whether and how expanding populations of mountain lions and humans will coexist, and what factors now regulate mountain lion populations. Although there is a significant accumulation of knowledge on mountain lion ecology at the population level (Anderson 1983, Lindzey 1987, and literature review sections of this ms.), I found no studies of how ecological or human factors affect mountain lion populations at a regional scale. Yet, increases in mountain lion abundance and distribution across western North America suggest a single or shared phenomenon operating at this scale.

Mountain lions may be one of the most difficult terrestrial mammal species to census (Logan et al. 1996). Most studies of mountain lion populations have occurred in areas where hunting did not occur or was greatly restricted (Hornocker et al. 1970, Lindzey et al. 1994, Logan et al. 1996). Managers of hunted populations must then make decisions in the face of chronic uncertainty with respect to how harvest affects vital rates and subsequent population growth. When animal populations are difficult to census, and management decisions must be made, focused population models offer a medium for testing hypotheses related to the effects of wildlife management on populations (Starfield 1996).

Concern for the welfare of large carnivores throughout North America has increased as has public desire to restore their role in western ecosystems (Kellert 1985, Noss et al. 1996). Concurrently, agricultural interests express concern about mountain lion depredation on their livestock, hunters worry about the effect large predators may have on game populations, and some homeowners are experiencing an unexpected threat to their pets and occasionally themselves. Balancing the concerns and interests for mountain lions among a multifaceted society requires data on stakeholders' beliefs, attitudes, and preferences for the species (Manfredo et al. in press). However, there are few such data sets to draw upon for large carnivores, generally (Kellert et al. 1996), and only one with regards to mountain lions (Zinn and Manfredo 1996).

Most mountain lion management has focused solely on our understanding of lion biology and behavior. A more comprehensive management approach includes integration of organismal and environmental aspects of mountain lion ecology with societal considerations of their

management (Decker et al. 1992, Ludwig et al. 1993, Meffe and Viederman 1995). Studying mountain lions in Montana provides an unprecedented opportunity to determine the ecological and human factors that led to population recovery of a large carnivore in human-dominated environments. From a conservation perspective, knowledge gained from understanding the factors facilitating mountain lion recovery should have utility in conservation planning for wild cats and other large carnivores (Fuller and Kittredge 1996). In addition, understanding factors that affect the distribution and abundance of mountain lions and how humans relate to an increase in the large cats will provide a scientific basis for more immediate lion management needs. A broad-based understanding of environmental factors influencing ecosystem functions is essential to an integrated ecosystem management strategy (Turner et al. 1994).

The purpose of an integrated analysis is to enlighten decisions and provide alternatives, not pat solutions (Goodwin and Wright 1991). In this manuscript, I have attempted to reduce the complexity of mountain lion management into 3 dimensions: environmental, biological, and human. Each dimension as it pertains to mountain lions is addressed in a separate chapter. The chapters are organized as separate papers on each management dimension. Chapter 6 discusses integrative management, and several examples of integrating the information about each dimension into comprehensive approaches for lion management. Additional data and findings are presented in the appendices.

Based upon my analysis, knowledge gaps that should be addressed by further research are identified and prioritized in Appendix I. Data on the historical abundance of mountain lions in Montana are presented in Appendix

III. Methods used to build a terrain ruggedness model are described in Appendix III. The mail questionnaire used to determine factors affecting stakeholder preferences for mountain lion populations is in Appendix IV.

CHAPTER TWO

STUDY AREA

All lands in Montana, except those within national parks and Indian reservations, served as the study area. Montana is the fourth largest state in the United States with a land area of 381,086 km.² Montana averages approximately 870 km. from east to west and 450 km. from north to south. It is bordered on the north by Canada, Wyoming to the south, Idaho on the west, and North Dakota and South Dakota on the east.

The average elevation in Montana is 1031 m. Elevations range from 546 m. where the Kootenai River exits the state in the northwest corner to 3898 m. in the Beartooth Mountains of south central Montana. Montana's western third is mountainous and the eastern two-thirds are a mix of undulating, cleft prairie and agriculture interspersed with rivers and isolated mountain ranges of the Missouri and Yellowstone watersheds (Figure 1.1).

The continental divide meanders south through Glacier National Park and the Great Bear-Bob Marshall-Scapegoat Wilderness nearly to Helena before turning southwest to form the Montana-Idaho border until it reaches Yellowstone National Park. The major watersheds west of the divide combine to form the headwaters of the Columbia River, and are comprised of the Bitterroot, Clark Fork of the Columbia, Flathead, and Kootenai River systems. East of the divide, the Missouri and Yellowstone watersheds form on the continental divide and flow east where they converge on the North Dakota border near Culbertson.

I divided the state into 3 mountain lion ecoregions based upon vegetation types and relative density of lions: the Montane, Intermountain, and Prairie Ecoregions. The Columbia Basin in northwestern Montana is dominated by the Northern Rocky Mountain-Steppe-Coniferous Forest-Alpine Meadow Province (McNab and Avers 1994). For purposes of my study, I grouped areas with a majority of Northern Rocky Mountain-Steppe-Coniferous Forest-Alpine Meadow Province within a hunting district (HD) into the Montane Ecoregion.

The southwestern portion of Montana and the Rocky Mountain East Front, an area encompassing the headwaters of the Yellowstone and Missouri Rivers, are classified as a mix of Middle Rocky Mountain Steppe-Coniferous Forest-Alpine Meadow and Southern Rocky Mountain Steppe-Open Woodland-Coniferous Forest-Alpine Meadow Provinces. This area was reclassified for this study into the Intermountain Ecoregion. A small portion of Intermountain Semi-Desert Province covers south central Montana east of the Beartooth Plateau. The remainder of the state is predominately Great Plains-Palouse Dry Steppe Province. Those habitats were grouped into a Prairie Ecoregion. This classification scheme follows one derived by the Montana Fish, Wildlife and Parks ecoregion classification (<http://nris.mt.gov/nsdi/nris/lu26.E00>) used to guide that agency's management.

Land-use within the Montane Ecoregion is dominated by commercial forestry and recreation associated with public lands (<http://nris.mt.gov/nsdi/nris/lu25/lu25e.html>). The Intermountain Ecoregion has a mix of commercial livestock grazing, farming (primarily wheat and barley) in the valleys, and forestry, mining, and recreation associated with national forest lands in the mountainous portions. Agriculture, primarily livestock grazing and dryland farming, dominate the landscape in the Prairie

Ecoregion. Water systems have been developed in many areas to facilitate irrigated alfalfa hay and food crops. Since World War II, domestic sheep numbers in Montana have declined by a factor of 10 while cattle numbers more than doubled (Montana Agricultural Reporting Service 1995). The estimated number of sheep in 1940 was 3,747,000; by 1994 sheep numbers had declined to 534,000. Cattle numbers increased over the same time period from 1,148,000 to 2,550,000.

Montana is occupied by a rich diversity of wildlife species. White-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and elk (*Cervus elaphus*) comprise the majority of prey for mountain lions, both in frequency and biomass (Murphy 1983, Williams 1992, Hornocker et al. 1992). Historically, white-tailed deer were restricted to northwest Montana and the mainstem Missouri River watershed in north central Montana (Mussehl and Howell 1971:69-80). White-tailed deer increased their distribution throughout nearly all major watersheds 1971-1995 and now occur in 100% of Montana counties. Densities are greatest in the Montane Ecoregion of northwest Montana, and least in the Prairie Ecoregion. Mule deer occupy 100% of Montana's counties, but are restricted primarily to rugged habitats, reaching highest densities in the Intermountain Ecoregion (Mackie et al. 1998). Elk have increased in abundance in all areas of Montana, but relatively recently have reoccupied the Prairie Ecoregion. They reach greatest abundance in the Intermountain Ecoregion, but also occur locally in high densities in the Montane Ecoregion within the Bitterroot and Clark Fork watersheds. Bighorn sheep (*Ovis canadensis*) distribution is patchy throughout western Montana, but bighorns can comprise a large seasonal component of a lion's diet (Williams 1992). Moose (*Alces alces*), mountain goats (*Oreamnos americanus*), and

pronghorn antelope (*Antilocapra americana*) live in areas occupied by mountain lions, but are seldom taken as prey (Anderson 1983).

The estimated human population in Montana during 1994 was 856,100 (2.3/km²) and exhibited an annual growth rate of 1.7%. The US growth rate for the same period was 1.2%. Eight of 10 Montana counties with the greatest human populations and highest growth rates are in the Montane and Intermountain Forested Grassland Ecoregions across the western third of the state. The Montane Ecoregion supports 34% of Montana's total population while 48% live in the Intermountain and 18% in the Prairie Ecoregions. A human demographic shift out of the prairie and into mountainous regions is occurring and is consistent with recent human migration patterns in other Great Plains-Rocky Mountain states (Riebsame et al. 1994).

The sociocultural environment of Montana during the last quarter of this century has been described as a "steady state in transition" (Center for National Policy 1992). Data from Montana's Bureau of Business and Economic Research (1995) supports the hypothesis of increasing sociocultural change. Montana's cities are now growing much faster than rural communities. The 5 greatest economic sectors in Montana are the same as in the past: agriculture, construction, manufacturing, transportation and trade. However, the fastest growing sectors in the 1990s were real estate, motion pictures, recreation, securities/commodities, and agricultural services (Montana's Bureau of Business and Economic Research 1995). Montana's per capita income was 81% of the national average, down from 88% in 1980 as the service industry takes on a larger portion of the economy.

Montana outpaces the national growth rates for numbers of gourmet coffee shops, art galleries, microbreweries, and cowboy poetry festivals

(Riebsame 1997). These secondary indicators suggest a change in the cultural landscape associated with internal and external migration into new areas of Montana (Bureau of Business and Economic Research 1995). A shift in human demographics generally leads to associated shifts in beliefs and attitudes towards the environment and land-use practices (Riebsame et al. 1994). However, quantitative socioeconomic data to support this hypothesis are lacking.

CHAPTER THREE

FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF MOUNTAIN LIONS (*PUMA CONCOLOR*) IN MONTANA.

INTRODUCTION

Mountain lions (*Puma concolor*), historically the most widely distributed terrestrial vertebrate species in the western hemisphere (Nowell and Jackson 1996:131-133), were eradicated in most of the Americas by 1930 (Young and Goldman 1946). Since the early 1970s, however, mountain lion distribution and abundance increased throughout western North America (Padley 1997:97-124). Mountain lions are now reported in the Great Plains (Genoways and Freeman 1996) and areas where they were historically rare or absent (Nero and Wrigley 1977, Berger and Wehausen 1991). Presently mountain lions are 1 of 2 large felids (i.e., mean adult weight > 20 kg), globally, to increase their distribution and abundance in the face of expanding human populations; the other species is the leopard (*Panthera pardus*) in parts of Africa and India (Nowell and Jackson 1996:3-4). The mountain lion's ability to flourish has created many opportunities, challenges, and problems for wildlife managers. Recent increases in negative mountain lion-human incidents (Beier 1991, Riley and Aune 1997) quickly elevated mountain lion management into political arenas (Stevens 1994), and raised questions about what factors regulate populations.

The density of most large carnivores is hypothesized as a function of metabolic needs and prey availability (Gittleman and Harvey 1982). Seidensticker et al. (1973) hypothesized that the density of mountain lions specifically is a function of vegetative cover, terrain variability, prey

abundance, and prey vulnerability related to prey behavior. Energy costs associated with intraspecific competition for a home range set density limits of a population. Subsequent research provides support for this hypothesis at a spatial scale equivalent to their respective study areas (Logan 1985, Lindzey et al. 1994, Logan et al. 1996)., The scale of inquiries to improve wildlife management decisions should match the scale of ecological phenomena that are studied and the scale of management decisions (Bissonette 1996). Increases in mountain lion abundance and distribution across western North America suggest a single shared phenomenon operating at a very broad scale.

No other issue in large carnivore management is as poorly understood or as controversial as the relationship between humans, carnivores, and mutually desired prey species such deer or elk (Estes 1996). An understanding of the interactions between mountain lions, habitat, and prey at the regional scale provides a basis for making management decisions about how to conserve mountain lions. However, few data are available to determine the effects of humans on mountain lions. Human populations and associated disturbances are hypothesized to diminish demographic resiliency of large carnivore populations (Weaver et al. 1996), but a test of this hypothesis at a regional level is lacking.

Studying mountain lions in western North America provides an unprecedented opportunity to determine ecological factors that contribute to the restoration of a large carnivore in human-dominated environments. Knowledge gained from understanding the environmental factors associated with mountain lion abundance should aid in conservation planning for felids and other large carnivores (Clark et al. 1996, Fuller and Kittredge 1996). My objective was to determine if models derived from empirical field studies correctly predict lion abundance at a landscape and regional level in Montana. Montana was selected

as a study area because its diversity of ecological communities and prey species is typical of many western ecosystems.

LITERATURE REVIEW

Mountain lion ecology and management were reviewed previously by Young and Goldman (1943), Anderson (1982), Lindzey (1987), and Hansen (1992). The review here is limited to more recent literature and findings relevant to the focus of my study.

Distribution

At least 30 subspecies of mountain lions have been classified from northern British Columbia to the southern tip of South America (Anderson 1983:4). The current hemispheric distribution has become patchy with the loss of populations in eastern North America and throughout much of central America (Lindzey 1987:657).

As late as 1850, mountain lions were common in the eastern deciduous forests of the United States (US), but with the exception of the Florida panther, their distribution was restricted to west of the Great Plains by World War II (Eaton 1973). Mountain lion populations currently are expanding throughout western North America (Padley 1997), and are present in many habitats where they were historically rare or absent (Berger and Wehausen 1991). In addition, a general eastward range expansion is occurring into the plains states (Genoways and Freeman 1996, Harveson 1997).

Historically, mountain lions probably were found in all habitats of Montana except open plains and prairies (Young and Goldman 1943). Lewis and Clark recorded their first observations of mountain lions in the Missouri

River Breaks, approximately 300 km east of the Montana Rocky Mountain Front (Coues 1893). Early bounty records indicate lions were present in 1900 as far east as present day Dawson County in the Yellowstone watershed and Hill County in the Missouri watershed (Appendix II -- in construction). By 1930, the known distribution of mountain lions in Montana was restricted to west of the continental divide and along the Beartooth-Absaroka plateau in southwest Montana. Mountain lions expanded their distribution in Montana after World War II, and by 1991 occupied 42 (75%) of 56 counties (Riley 1992). A similar increase in distribution is reported in nearly every western state and province (rev. Braun 1991, Padley 1997).

Habitats

Mountain lions occupy a variety of habitats from arid deserts to tropical rain forests (Nowell and Jackson 1996:132). However, mountain lions do not use vegetative or topographic features in proportion to availability (Logan and Irwin 1985, Laing and Lindzey 1991, Williams 1992). Mountain lions mostly select habitats with dense cover and rugged terrain.

Seidensticker et al. (1973), Logan and Irwin (1985), and Laing (1988) report the most favorable habitats are those with dense understories. In Montana, Williams (1992) found the highest summer densities of mountain lions were associated with coniferous habitat types. Vegetation provides stalking cover for hunting (Hornocker 1970), cover for uninterrupted food consumption (Logan and Irwin 1985), and security for kittens (Seidensticker et al. 1973). Whereas mountain lions may live in areas free of over-story vegetation (Laing and Lindzey 1991), larger home ranges and lower densities are associated with deserts and grasslands (rev. by Anderson 1983:48, 62).

Regardless of vegetative cover, increased lion densities appear associated with terrain described as “highly variable” (Seidensticker et al. 1973), “high relief” (Gonyea 1976), “canyonlands” (Logan 1985), “interspersed ledges” (Laing and Lindzey 1992), and “steep and rugged” (Williams 1992:38). Williams (1992) was the only researcher to define and quantify habitat ruggedness for mountain lions using a land surface ruggedness index developed by Beasom (1983). He found a parabolic relationship where mountain lions used moderately rugged terrain more than level or very steep/rugged terrain.

Physical specialization within the family Felidae are adaptations to each species’ unique mode of attack and their prey’s behavior (Vaughan 1978:223). The morphological characteristics of mountain lions are evolutionary expressions of a carnivore adapted for stealth hunting in habitats with topographical diversity and cover (Gonyea 1976). They have large feet and proportionally the longest posterior limbs of any felid (Gonyea 1976).

Prey

Throughout the northern Rocky Mountains, ungulates such as mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (*Cervus elaphus*) are the primary prey of mountain lions (Anderson 1983). Where other species such as bighorn sheep (*Ovis canadensis*) are locally abundant, they are readily taken by lions (Berger and Wehausen 1991). Ross et al. (1997) found that ungulates provided at least 99% of the biomass consumed by mountain lions in the November-April period.

A particular prey species may vary in importance with location. Hornocker et al. (1992) indicated mule deer were a preferred prey, but found

elk most commonly taken by mountain lions in northern Yellowstone National Park. Williams (1992) found that deer, elk, and bighorn sheep comprised 43%, 27%, and 18%, respectively, of the lion's diet on the East Front of the Rockies. Similar reports were made by Ross and Jalkotzy (1992) for the southwest Alberta Front Range. In western Montana, however, Murphy (1983) indicated white-tailed deer were the species most common in the lion's diet.

Abundance

Lindzey et al. (1994) suggested that environmental factors important in determining cougar density change over time, making it difficult to define the relationships between mountain lions and their prey. The density of carnivores is hypothesized as a function of metabolic needs and prey availability (Gittleman and Harvey 1982). Prey distribution and abundance also strongly influences carnivore spatial organization (Kleiman and Eisenberg 1973) and density (Sunquist and Sunquist 1989).

Density of lions was hypothesized by Seidensticker et al. (1973) as a function of the total combination of vegetation, terrain, prey numbers, and prey vulnerability. However, those authors provided only a qualitative model of the proposed relationship. Vulnerability refers to the ease with which prey can be captured, killed, and consumed by lions and is a function of a habitat's structural composition and prey behavior (Seidensticker et al. 1973). Subsequent research supports the hypothesis that mountain lion density is regulated by environmental factors other than prey abundance (Logan 1985, Lindzey et al. 1994, Logan et al. 1996). Hornocker (1970, 1976:109) suggested habitat characteristics ultimately determine carrying capacity for prey and hence lions. He offered a simple conceptual model that describes his

interpretation of mountain lion habitat-prey relationships: “habitat → mule deer [ungulates] → lions.” Based on this research, I propose the model can be expanded to: cover + terrain → habitat → ungulates → lions. However, I found no previous research that has tested either model at the landscape or regional scale.

Mountain lions are one of the most difficult terrestrial mammals to census (Lindzey 1987). No reliable enumeration techniques exist that do not require extraordinarily intensive field efforts (Smallwood and Fitzhugh 1995), and these techniques are logistically impossible to conduct over an entire state such as Montana. Difficulty in censusing mountain lions has precluded analyses of populations at scales other than one or a few mountain ranges. In the absence of a rigorous census techniques, an index of abundance can be used to make landscape level inquiries into population ecology (Caughley 1977:12).

Humans

The relationship between humans, anthropogenic disturbance, and mountain lions is unclear. A dearth of research exists on the effects of human disturbance to mountain lions. Large carnivores decreased in distribution and abundance following European settlement (Fuller and Kittredge 1996, Paquet and Hackman 1995). The population resilience of large carnivores to human disturbance is hypothesized as low (Weaver et al 1996). A frequent paradigm associated with mountain lions is reflected in common descriptions for the species. Cahalane (1964) indicated that survival of the lion depended on sufficient wilderness, while popular books and videos (McCall and Dutcher 1992) label the mountain lion “Ghost of the Rockies”. However, these views are not supported by recent increases in lion populations throughout the West.

METHODS

My objective was to investigate factors that affect the distribution and abundance of mountain lions, and construct models with biologically meaningful data that predict their abundance in Montana. Based on findings from small scale, empirical studies (Seidensticker et al. 1973, Lindzey et al. 1994, Logan et al. 1996), I used extant landscape and regional-scale data to examine hypotheses regarding environmental variables thought to most influence mountain lion populations. I compared the relative abundance of mountain lions with measures of habitat, humans, and prey abundance at landscape and regional scales. Bissonette (1996) discussed in detail the need to match scales of inquiry to scales of management decisions. My analyses were conducted at the scale of hunting districts (HD) and ecoregions within Montana, the scale that state management decisions about mountain lion populations occur. The time period of analysis was 1 July 1971 - 30 June 1994. These years represented the most consistent and accurate data on mountain lion mortality.

Mountain Lion Abundance

An index of abundance for mountain lions (TMI) was derived from the density of total mountain lion mortality (mortality/km²) at the HD level. Hunting districts ranged in size from 320 km² to 7012 km² (\bar{X} = 1550 , SE = 171). Thirty-four HD were used that maintained consistent boundaries through time and were distributed across Montana. I assumed TMI was correlated to lion abundance at a large scale; if lion abundance increased, then I expected a

corresponding increase in total mortality. Mortality records were derived from Montana Fish, Wildlife and Parks databases (Aune and Schladweiler 1994). All mountain lion deaths in Montana are required by law to be reported and inspected by the state wildlife agency. I only used records with a known location of death.

Potential biases associated with a mortality index are related to hunter selection for certain sex or size (Jalkotzy et al. 1996), weather that influences hunting success (Murphy 1983), and other environmental factors such as the distribution of livestock that may lead to increased animal damage control action (Aune and Schladweiler 1994).

Habitat

A variable HABITAT was derived by multiplying an estimate of terrain ruggedness of an area by the proportion of that same area in habitat types associated with dense understory cover. A terrain ruggedness index (TRI) was computed from 1:24000 digital elevation maps using an ARC/INFO geographical information system (GIS). I used PROC DOCELL to calculate the sum change in elevation between any pixel (1 km²) and its 8 neighboring pixels (Appendix III). A mean TRI value was derived for each hunting district by calculating a mean of all pixels encompassed by a the district.

I then compiled a GIS data set, or coverage, of climax vegetation developed by Montana Fish, Wildlife and Parks ecologists (<http://nris.mt.gov/nsdi/nris/lu26.E00>). The coverage is currently used for statewide wildlife plans. Based on Bailey's classification (McNab and Avers 1994), that approximates the FWP scheme at the biome level, I assumed the Montane Forest and Plains Forest habitat types were the only types that

consistently contain sufficient concealment cover required by mountain lions for efficient stalking of prey and security.

The TRI for a unit of land was then multiplied by the proportion of the unit in forested cover types to create the coverage, HABITAT. Areas with no forested habitats were given values of 0.01 to avoid creation of regression variables with a value of 0. Values of HABITAT increased from a base value of $0.01 \times \text{TRI}$ in areas without forested cover to $1.0 \times \text{TRI}$ in areas with 100% forested cover.

Humans

A GIS coverage of human population was generated by linking 1990 block-group level census data to census geography existing in the US Census Bureau TIGER files (USCB 1991). Estimates of human density for each HD were created using ARC/INFO GRID. A grid with 1 km cell sizes was overlaid on a map of census blocks. A density estimate was then derived for each cell within each HD. A mean HD density was calculated by dividing the sum human population by the area of the HD.

Prey

TMI was compared with indices of prey abundance derived from adult buck harvest for mule deer (MD) and white-tailed deer (WTD), and total harvest for elk (ELK) at the hunting district level. These measures are generally robust enough to follow population trends (Roseberry and Woolf 1991) and the only consistent measures of ungulate abundance in all areas of Montana.

Statistical Methods

I tested the hypothesis that a significant positive relationship exists between HABITAT and the abundance of mountain lions using linear regression. An arcsine square root transformation ($Y_i = \arcsin(Y_i)^{1/2}$) of lion density was used to adjust the proportions to a normal distribution (Zar 1984:239-241). The arcsine square root of TMI was the dependent variable and HABITAT was the independent variable. The regressions were run using a mean 1992-1994 TMI for a HD. The 3-year mean reduces bias that might be introduced from variation in factors affecting mountain lion mortality in any one year.

To investigate the hypothesis that a significant negative relationship exists between humans and mountain lions, I regressed the arcsine-square root transformation of TMI against the density of humans (HUMANS).

Regressions were then conducted using the arcsine square root of TMI as the dependent variable and MD, WTD, and ELK as independent variables. A comparison of TMI and ungulate abundance was made between 34 mountain lion hunting districts across Montana. Regression analyses were also run for years 1978-1994 to determine temporal relationships within each Ecoregion.

Model Development

Multiple regression analysis was used to construct a model that predicted mountain lion abundance within Montana. The arcsine square root of TMI was used as the dependent variable and HABITAT, HUMANS, MD, WTD, and ELK were independent variables. To identify the most parsimonious model (Neter et al. 1990), I used an optimum-subsets selection that minimized the Mallows C_p statistic (Mallows 1973).

RESULTS

Lion Abundance

Records of 4,057 mountain lion deaths from 1971-1994 were examined. Statewide annual mortality ranged from 51 in 1971 to 600 in 1994 (Figure 3.1). Mortality levels increased gradually from 1971-1988 and then increased rapidly through 1994. Hunting was the single greatest cause of known mortality in all years ($\bar{X} = 92.6\%$, Range = 80.0 - 99.2%).

TMI was greatest in the Montane Ecoregion, but the percentage of the total statewide TMI comprised by the Intermountain type increased after 1975. Mountain lions only recently re-appeared in mortality records from the Prairie Ecoregion of eastern Montana. The 1992-1994 average mortality density for the Montane, Intermountain, and Prairie Ecoregions was 0.017, 0.007, and 0.008 lions/km², respectively. The 1992-1994 average HD TMI ranged from 0.052/km² in northwestern Montana to 0.0005/km² in southeastern Montana (Appendix III).

Habitat

Values for TRI, forested cover, and subsequently HABITAT generally increased from east-to-west and south-to-north across Montana. Ecoregion mean TRI values were 942.1 (SE = 47.4), 659.9 (SE = 40.9), and 226.6 (SE = 44.9) for the Montane, Intermountain, and Prairie Ecoregions. The statewide mean was 616.7 (SE = 29.1). For areas with mountain lions the mean was 776.6 (SE = 35.1) and for areas without lions the mean was 192.6 (SE = 21.9).

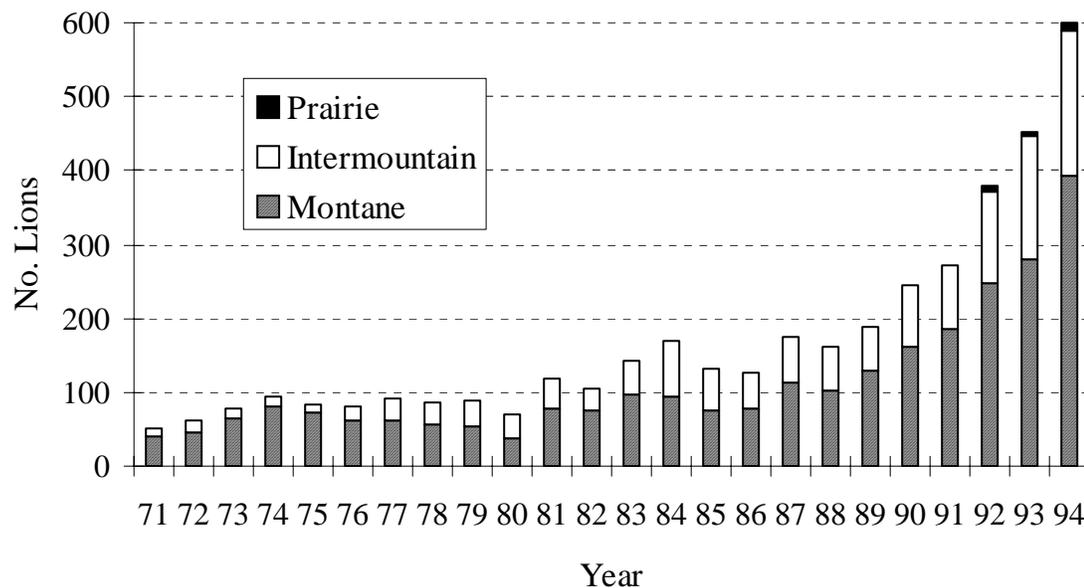


Figure 3.1. Mountain lion mortality in the Montane, Intermountain, and Prairie Ecoregions of Montana, 1971-1994.

The distribution of forested habitat types statewide is similar to the distribution of TRI values. The forested areas of Montana tend to be the more rugged. Ecoregion means were 82.6% (SE = 3.7), 41.8% (SE = 3.0), and 3.2% (SE = 1.8) for the Montane, Intermountain, and Prairie Ecoregions; and the state mean was 64.7% (SE = 5.1) for areas with lions and 4.2% (SE = 1.9) without lions.

A strong linear relationship ($r^2 = 0.73$, $p < 0.001$) was detected between HABITAT and TMI (Figure 3.2). HABITAT values ranged from 851.7 for the Montane Ecoregion to 25.9 for the Prairie. The Intermountain Ecoregion had intermediate values of 331.3. Across Montana, means were 603.1 (SE = 67.0) for those areas with mountain lions and 7.6 (SE = 3.3) for areas without lions. Within the Montane Ecoregion, HABITAT was closely associated with TMI

($r^2 = 0.55$, $p = 0.001$). However, the relationship was weaker within the Intermountain Ecoregion ($r^2 = 0.20$, $p = 0.09$).

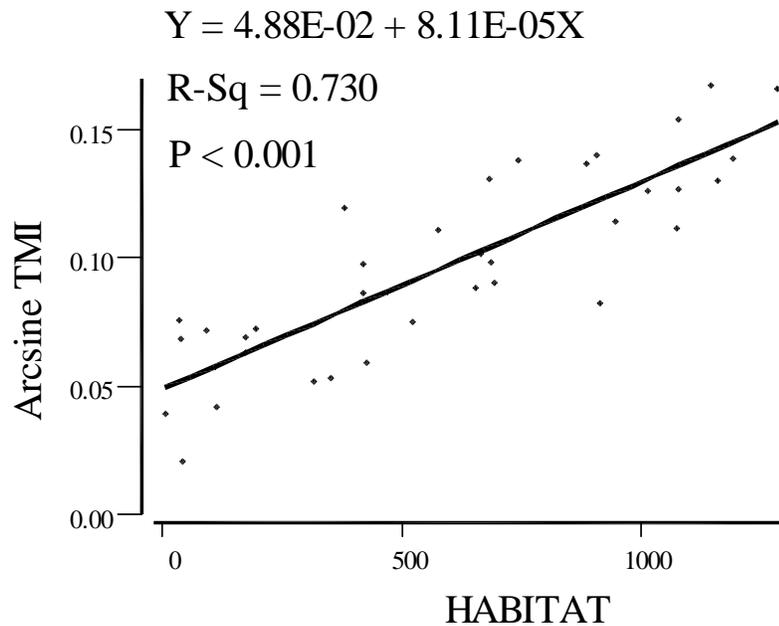


Figure 3.2. The relationship between HABITAT and the total mortality index of mountain lions in Montana. HABITAT was the product of a terrain ruggedness index and the proportion of a hunting district in forested habitat types.

Humans

No significant relationship was detected between human and lion densities ($r^2 = 0.05$, $p = 0.208$). However, ecoregions in Montana with the highest densities of humans have the highest TMI. The human densities were 4.14, 3.05, and 0.79/km² for the Montane, Intermountain, and Prairie Ecoregions.

Prey

Across Montana, a linear relationship existed between TMI and WTD and ELK, but no significant relationship was discernible with MD (Figure 3.3). The most parsimonious model to predict TMI included the variables WTD and MD ($r^2 = 0.54$, $p < 0.001$), where $TMI = 0.96 + 0.014WT - 0.014MD$. Elk abundance alone accounted for only a small amount of the variance in lion abundance statewide ($r^2 = 0.03$, $p = 0.29$).

There was a strong linear relationship between overall ungulate abundance and TMI through the time period 1978-1994 (Table 3.1). The ungulate species most important in affecting the variation in lion density, however, varied with ecoregion. Within specific ecoregions, increased white-tailed deer abundance was linearly related with TMI in the Montane type west of the continental divide (Figure 3.4). However, ELK and TMI were most closely associated in the Intermountain Ecoregion (Figure 3.5). Mountain lions have not occupied the Prairie Ecoregion long enough or at high enough densities for a causal relationships with prey to be detected.

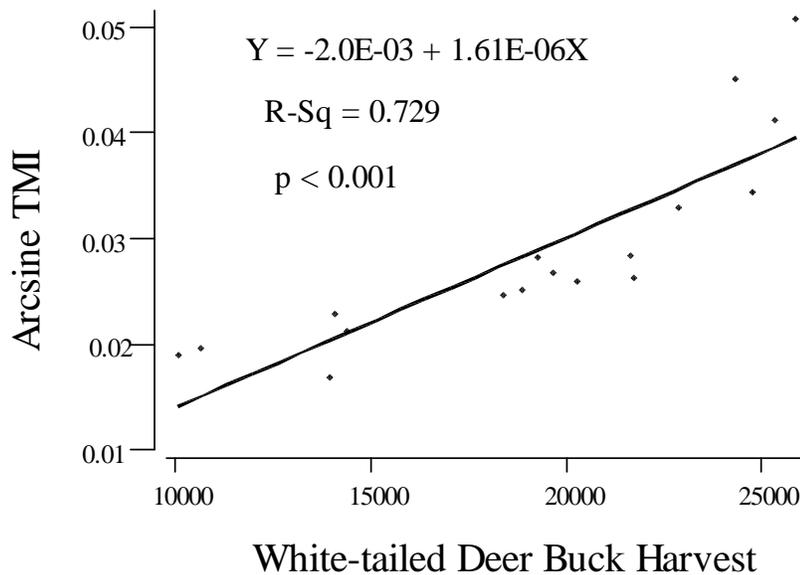
Table 3.1. Regression coefficients that describe the relationship between mountain lion and ungulate indices of abundance in Montana, 1976-1994. P-values shown in parentheses.

Ecoregion	White-tailed Deer	Mule Deer	Elk
Montane	0.826 (< 0.001)	0.258 (0.053)	0.409 (0.006)
Intermountain	0.455 (0.006)	0.115 (0.215)	0.639 (<0.001)
Prairie	0.599 (0.071)	0.384 (0.189)	*
State	0.750 (<0.001)	0.096 (0.262)	0.663 (<0.001)

* No elk present.

Prey and Habitat

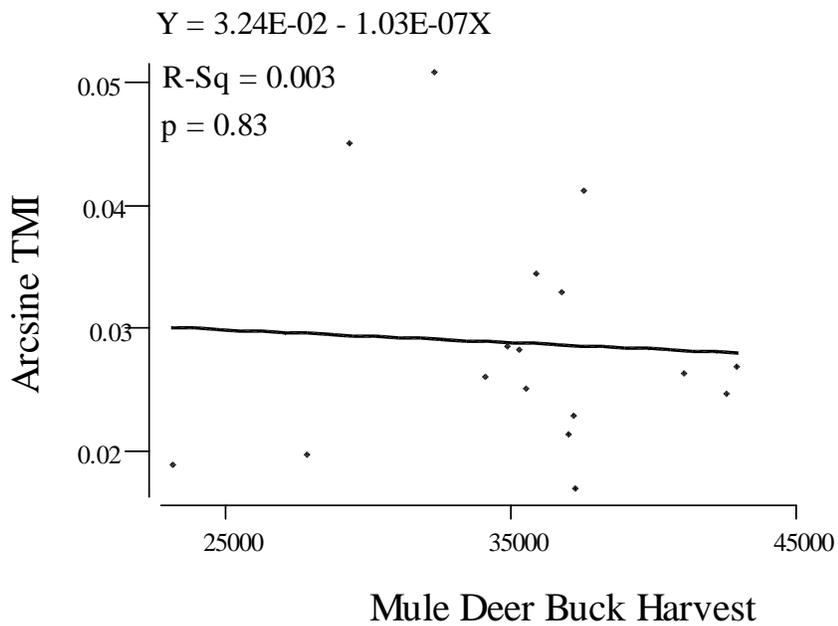
A 2 factor model ($TMI=0.0428+0.007WT+0.00006HABITAT$, $r^2 = 0.78$, $p < 0.001$) was the most parsimonious model for prediction of TMI on a state-wide basis. The r^2 value was increased < 0.01 when MD and ELK were added to the model. The same 2-factor model on a statewide basis is also the most efficient model to explain variation in TMI values within the Montane Ecoregion. However, this relationship is not statistically significant within the Intermountain Ecoregion.



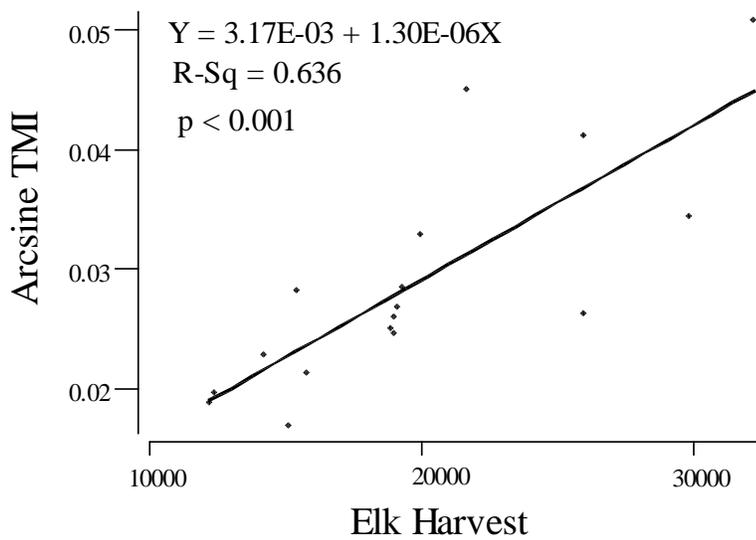
(a)

Figure 3.3. The relationship between the state-wide total mortality index for mountain lions in Montana and a) white-tailed deer buck harvest, b) mule deer buck harvest, and c) elk harvest. Data are for mountain lion hunting districts.

Figure 3.3 (Continued)



(b)



(c)

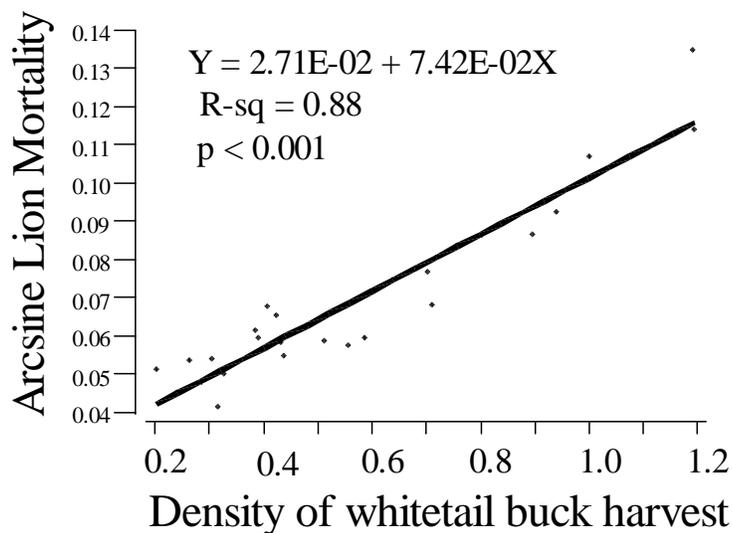


Figure 3.4. The relationship between the total mortality index for mountain lions and density of buck white-tailed deer harvest in the Montane Ecoregion of Montana, 1978- 1994. Data are for mountain lion hunting districts.

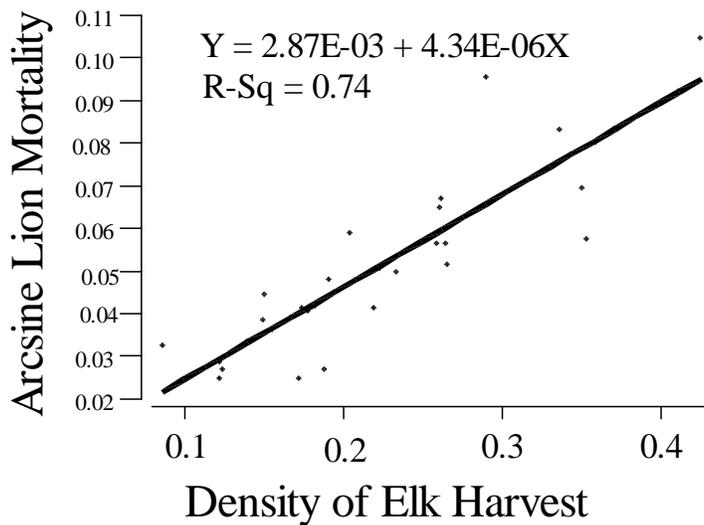


Figure 3.5. The relationship between the total mortality index for mountain lions and density of total elk harvest in the Intermountain Ecoregion of Montana, 1978- 1994. Data are for mountain lion hunting districts.

DISCUSSION

My findings fail to reject the hypotheses that cover and terrain function to define habitat quality for mountain lions. Forested cover in combination with topographic heterogeneity leads to higher densities of mountain lions if all other variables are constant. However, the third variable, prey, is seldom constant. An interaction between habitat quality and prey abundance accounts for the variability in mountain lion populations. These data substantiate, at landscape and regional scales, the conclusions of previous research at the population level (Seidensticker et al. 1973, Logan 1985, Logan et al. 1996).

Lack of a clear relationship between relative densities of mountain lions and mule deer is inconsistent with my initial hypothesis that mule deer and mountain lion densities would be highly correlated. There are several potential explanations for this contradiction.

First, the importance of mule deer in the mountain lion's diet was emphasized in early studies throughout the West (Anderson 1983:50-54). Many of these studies were conducted where mule deer were the only prey effectively available to mountain lions. Where mountain lions occur with multiple options for prey, species other than mule deer may take on greater importance (Ross and Jalkotzy 1997, Iriarte 1990). Even in traditional mule deer habitats such as those found on the East Front of the Rockies, elk are often the most frequently taken prey species, and white-tailed deer now comprise more of the mountain lion's summer diet there than mule deer (Williams et al. 1995).

Second, there may be factors constraining mule deer populations, but favoring white-tailed deer and elk (Mackie et al 1998). Mule deer occupy environments more susceptible to periodic decimating factors such as drought

and winter severity (Logan et al. 1996, Mackie et al. in press). Hence, mule deer populations have fluctuated the past 30 years while white-tailed deer, elk and mountain lion populations steadily increased. A surge in white-tailed deer abundance, especially in the Intermountain and Prairie Ecoregions, occurred since the time when mountain lions were scarce or nonexistent during the 20th century. The distribution and abundance of elk have also increased substantially because of favorable habitat conditions and conservative game management.

The expansion of mountain lion populations since World War II probably began from refugia provided for both the lion and its prey by the dense forests and rugged terrain of northwestern Montana. Habitats west of the continental divide support the highest densities of mountain lions. These areas also accounted for the highest take of lions in the early 1900s . The Montane Ecoregion was also the last place to record a take of mountain lions under the bounty system, long after populations had been extirpated from the Intermountain and Prairie Ecoregions.

Weaver et al. (1996), suggested mountain lions and other large carnivores have low demographic resiliency in the face of human disturbance. Humans normally cause the greatest number of adult mountain lion deaths in hunted populations (Anderson 1983:68, Lindzey 1987, Ross and Jalkotzy 1992). Montana is not an exception. However, the 600 mountain lions killed in Montana during 1994 is 3.6 x greater than the highest annual mortality when the bounty system was thriving. The 1994 mortality level was also preceded by 5 years of increasing mortality, and 7 years of mortality levels greater than the highest bounty take. There must be greater demographic resiliency in mountain lions today than existed in the late 1800s and early 1900s to support the

observed level of mortality. Factors that are influencing an apparent increased resiliency in lion populations may provide lessons for carnivore conservation elsewhere.

Mountain lions are limited in part by habitat characteristics of the landscape (Hornocker 1970, Seidensticker et al. 1973). There are many places in Montana with abundant prey resources, but few or no mountain lions. Habitats in those areas, typically prairies, are characterized by either level terrain or a lack of forested cover. In cases where mountain lions are found in prairie environments, they are associated with riparian forest communities (Williams 1992). The first accounts of mountain lions in Montana were along the timbered water courses of the Missouri River (Young and Goldman 1946).

The terrain in Montana has not changed significantly since the last glaciers (Pielou 1992). Forested cover has changed locally with fire suppression, timber cutting, agricultural development, and grazing (Gruell 1983). However, while the distribution of general forested habitats at a broad scale probably has not been altered, prey populations have changed through time. There is no place in Montana that supports a population of mountain lions that does not also support deer or elk.

Food web theory provides some clue to what caused an increase in mountain lions in the face of considerable human-caused mortality. I hypothesize that human-induced changes to the environment and lowest trophic levels (McDonald and Pickett 1993) have provided for a positive bottom-up influence on mountain lion populations. Food web theory suggests that as either the number of lower trophic level species or abundance of any particular species increases, top level species should increase through bottom-up influences (Hunter and Price 1992). The establishment of white-tailed deer in

previously unoccupied habitats east of the continental divide in Montana increased the number of available lower trophic species and increased the distribution of that level's biomass. White-tailed deer adapt well to humans and may actually increase with human disturbance (Waller and Alverson 1997). Similarly, elk and bighorn sheep have flourished in Montana when reintroduced into habitats not occupied since the mountain lion population lows of the 1930s.

We need to understand what has affected ungulate populations at a landscape level to better understand the environmental factors that have influenced mountain lion populations through time. Plants have primacy in food webs (Power 1992). In the arid western environment nitrogen and water are generally limiting. Anthropogenic inputs of nitrogen and phosphorus to landscapes increased dramatically post World War II (Smil 1990). Ammonia fertilizer applications have increased 20-fold since 1860 (Smil 1985). Water development in Montana, like most of the West, has focused on irrigation of arid lands to benefit crops and livestock (L'vovich and White 1990). In 1990, an estimated 34,264,536 L./day of water was used in Montana for irrigation (USGS 1991). Most of that irrigation is for alfalfa and hay crops that dot the landscape (Riebsame 1997). One result from these alterations to the system has been an increase in net primary production (Turner 1987). Another result in turn may be a greater number of lower level trophic species (e.g., ungulates) as well as a greater abundance of some species. Increases in the distribution and abundance of elk and white-tailed deer may be a response to broad effects on the base environment in Montana. Another outcome, in turn, may be an enhanced landscape for mountain lions and other large carnivores.

The factors that affect carnivore populations usually take place over a temporal scale of decades (Litvaitis et al. 1996). Time, and the recovery of

ungulates after the habitat alterations and meat harvests of the late 1800s and early 1900s (Wagner 1978), were apparently required to restore lion populations in Montana. Empirical research is needed to determine the ultimate causes for increases in ungulate populations that have lead to increased lion populations (Mackie et al. in press). Regardless of ultimate causes, it will be difficult to affect mountain lion populations over the short term through alteration of environmental factors. Mountain lion management in northern latitudes should always take into account issues affecting abundance and distribution of large ungulates (Iriarte et al. 1990).

CHAPTER FOUR

SENSITIVITY ANALYSIS OF A STOCHASTIC POPULATION SIMULATION MODEL FOR MOUNTAIN LIONS (*PUMA CONCOLOR*): IMPLICATIONS FOR MANAGEMENT.

INTRODUCTION

Mountain lion populations in Montana have flourished recently in response to favorable habitat conditions and increased prey abundance (Chapter 3, this ms.). One outcome has been negative lion-human interactions that have created a difficult operating environment for wildlife managers (Riley and Aune 1997). Management attempts to balance conflicting demands upon the mountain lion resource from a diverse array of stakeholders that includes hunters, livestock growers, animal protectionists, and homeowners throughout Montana (Montana Fish, Wildlife and Parks 1996). Demand for mountain lion hunting increased over 12% annually during 1971-1995 while agricultural interests voiced concern about increased livestock depredation from a perceived increase in predator abundance (Riley and Aune 1997). Mountain lions have preyed upon pets, and attacked several humans, including a fatal attack on an 8-yr.-old boy in 1989, and 2 serious maulings of children in Glacier National Park in 1991 and 1992. Concurrently, some stakeholders are calling for increased conservation measures to sustain large carnivore populations throughout the intermountain west (Noss et al. 1996).

To control depredations and provide hunting opportunity, the primary response of wildlife managers has been to increase hunting quotas for mountain lions and increase animal damage control actions. Harvest quotas increased from 194 to 505 (159%) between 1988 and 1995. Nearly 600 mountain lions

were killed through hunting and nonhunting causes in 1995. This number is at least 3.6 x greater than the highest recorded yearly take of lions during the years of the bounty system.

Mountain lions are one of the most difficult terrestrial mammals to census. Thus, wildlife managers must make decisions in the face of chronic uncertainty with respect to mountain lion populations. Focused population models offer a medium for testing hypotheses related to the effects of wildlife management on populations when a species is difficult to census (Starfield 1996).

Caughley and Sinclair (1994:2) indicate there are only 4 ways that a population can be managed: (1) make it increase; (2) make it decrease; (3) harvest it for a continuing yield; and, (4) leave it alone but keep an eye on it. Management action to achieve the first 3 goals generally strive to affect a population's growth by manipulating natality and mortality rate (McCullough and Barrett 1992). One technique to assess the relative importance of each vital rates is sensitivity analysis of population simulation models (Burgman et al. 1993:98-100). The importance of vital rates is measured by successively changing each rate and measuring the subsequent change in the observed growth rate of a population (r_0).

Another important use of this technique is in planning of optimal management strategies. A sensitivity study encourages the best investment of conservation dollars by focusing management action on the most important vital rates in a population or a species (Goodman 1980). The utility of sensitivity studies is exemplified by Marchall and Crowder (1996) for fish, Crowder et al. (1994) for reptiles, Heppell et al. (1994) for birds, and Escos et al. (1994) for mammals.

A measure of sensitivity alone, however, may not provide a robust index of each vital rate's effect on the finite rate of increase (λ). Sensitivity analysis enables a qualitative ranking of vital rates according to their relative importance in affecting λ . To quantitatively determine the relative importance of each rate, Wisdom and Mills (1997) suggested regression analyses be conducted using each vital rate as an independent variable and λ used as the dependent variable.

My objective was to determine the vital rates that most affect λ of mountain lions in Montana. A general model was also needed to test hypotheses related to mountain lion populations, and to demonstrate advantages or disadvantages of alternative management strategies.

LITERATURE REVIEW

The demographic properties of an animal population are determined by the life history patterns and behaviors of its members (Caughley 1977). Mountain lion populations are hypothesized to be self-regulated through a system of land tenure. The land tenure system results from mutual avoidance between individuals facilitated by visual and olfactory marks (Hornocker 1969, Seidensticker et al. 1973, Sweanor et al. 1996). Population growth occurs from production of cubs within a population or immigration from other populations (Logan et al. 1996).

Hornocker (1969) and Seidensticker et al. (1973), who studied the same mountain lion population in central Idaho, were the first to report on the function of the social system in regulating numbers of lions. Males occupied larger home ranges that overlapped minimally with those of adjacent resident males, but typically overlapped 2-5 female home ranges (Hornocker 1969,

Logan et al. 1996, Spreadbury et al. 1996). Unlike males, home ranges of adjacent females overlapped with each other. The amount of within gender overlap of home ranges increased and home range size diminished with increased population density (Sweanor et al. 1996).

Establishment of a home area among lions is reported as essential for both sexes to participate in breeding (Seidensticker et al. 1973, Spreadbury et al. 1996). However, a recent study by Hornocker et al. (1992) in Yellowstone National Park indicated a small portion of the breeding population can be transient, without establishing a true home area.

Adults generally represent the highest proportion of a mountain lion population. However, the imprecision associated with aging mountain lions, and different definitions of age classes, make comparisons and generalization difficult. Logan et al. (1996) found that adults, in a population manipulated by limited removal from simulated hunting, comprised 56% (SD = 13%) of the population. Adult females comprised 33% (SD = 8%) and adult males comprised 23% (SD = 7%) of the total population. Subadults were reported to comprise 7% (SD = 7%) and cubs 32% (SD = 10%). Adults comprised an even greater proportion of the San Andres Mountain population used as a reference to experiments. The mean proportions by age class were: total adults = 61% (SD = 9%), adult females = 35% (SD = 7%), adult males = 26% (SD = 3%), subadults = 6% (SD = 2%), and cubs = 33% (SD = 8%). Similar relative proportions were observed by Ross and Jalkotzy (1992) in a hunted Alberta population.

The mountain lion reproductive season is potentially year-round (Sweanor et al 1996, Ross and Jalkotzy 1992). However, most births occur in a period of 2-5 months during the warmest weather (Anderson 1983:32, Logan et

al. 1996). In Montana and other northern habitats, most lion births occur between June and September. Johnson et al. (in press) found that all known births in South America occurred in similar seasonal pattern, but between February and June.

Estrus is approximately 8 days (Anderson 1983:31) with cycles every 13-33 days in wild mountain lions (Logan et al. 1996). The gestation period for mountain lions averages about 92 days (Range = 84-98; Anderson 1983:33, Logan et al. 1996).

Litter size is difficult to determine in the wild because of the secretive behavior of female mountain lions. Observed litter sizes in the wild vary from 1-6 cubs with 2 or 3 cubs most common, followed by litter sizes of 4, 1, 5, and 6 in descending order of frequency (Anderson 1983:34, Lindzey et al. 1992, Ross and Jalkotzy 1992). Prenatal litter sizes are reported to average 3.4 cubs (Range = 1-6), however postpartum litters average 2.2 cubs (Range = 1-6) (Anderson 1983:34). The latter estimate is derived from litters of various ages and some neonatal mortality is suspected to have occurred before estimates were made. Logan et al. (1996) observed a mean litter size of 3.0 for 9-49 day old litters in New Mexico, and a mean of 3.1 cubs was observed by Spreadbury et al. (1996) in British Columbia. Logan et al. (1996) also observed a larger mean of 3.4 for first litters. Those researchers hypothesized that larger first litters may be a compensatory response to reduced adult populations.

Sex ratios of cub and early subadult mountain lions are commonly reported to approximate 50:50 (Anderson 1983:61, Logan et al. 1996, Spreadbury et al. 1996). Sex ratios in cubs generally favor males if the ratios are skewed. Lindzey et al. (1992) in southern Utah, and Ashman et al. (1983:19) in Nevada, detected a cub sex ratio of 1.3 M:1.0 F. However, late

subadult and adult sex ratios in lion populations normally favor females 2-5:1 (Hemker et al. 1984, Anderson 1983:61, Lindzey et al. 1992, Logan et al. 1996). The apparent change in sex ratios implies greater mortality of male subadults.

Mountain lions become independent of their mothers between 12 and 18 months (Ross and Jalkotzy 1992, Logan et al. 1996). Estimates vary depending upon definition of independence. Sexual maturity, as defined by timing of first male-female associations was estimated at 21.4 months for females and 24.3 months for males (Logan et al. 1996). These researchers reported a mean age of first reproduction of about 29 months (SD = 6.0). Ross and Jalkotzy (1992) reported the mean age of first parturition as 30 months in Alberta, and Lindzey et al. (1994) found a mean age of 26 months (SD = 4.5) in southern Utah. The range in ages of first reproduction in these field studies was 15-45 months. A high proportion of adult female lions within a population are involved in raising young at any given time. Logan et al. (1996) reported estimates of 73% involved in breeding, and Logan (1983) estimated 55% and 86% in two consecutive years.

The mean interval between births is normally reported to be 20 months (Range = 12-40 months). However, over 90% of reported intervals are between 15-25 months. A mean interval of 19.7 months was reported in southwestern Alberta (Ross and Jalkotzy 1992), 24.3 months in southern Utah (Lindzey et al. 1994), and 18.3 months in southeastern British Columbia (Spreadbury et al. 1996). Logan et al. (1996) reported a mean interval of 17.4 months where at least 1 cub survived to independence in New Mexico.

Causes of death vary between populations, but human-caused mortality is highest in nearly every reported case. Hunting is the primary cause of

mortality in hunted populations (Ross and Jalkotzy 1992, Logan et al. 1986), and control measures related to depredation management are a primary source of mortality in non-hunted populations (Weaver and Sitton 1978).

Accidents, intraspecific strife, and cannibalism are additional sources of mortality. Accidents related to killing prey or falling off ledges are common, but usually comprise fewer than 10% of the total deaths (Logan et al. 1996, Spreadbury et al, 1996). Mountain lion-vehicle collisions also occur. Spreadbury et al. (1996) indicated these accidents were the greatest source of mortality (4 of 7 lion deaths) in an un hunted population they studied. Aune and Schladweiler (1993) reported 13 mountain lion deaths due to vehicle collisions in Montana during the 1992-1993 period.

Intraspecific strife is reported in most studies of mountain lions (Hemker et al. 1984, Lindzey et al. 1989, Ross and Jalkotzy 1992, Beier and Barrett 1993, Spreadbury et al. 1996, Sweanor et al. 1996). Aggressive behavior may be the single greatest cause of death in lion populations isolated from humans (Logan et al. 1996). Males accounted for all the killing by conspecifics in the New Mexico population studied by Logan et al. (1996). Males killed all age classes and both sexes of mountain lions. Infanticide or cannibalism accounted for 44% of the known deaths among cubs. Hemker et al. (1984), Ross and Jalkotzy (1992), and Spreadbury et al. (1996) reported evidence of mortality from intraspecific strife elsewhere. Males, through territoriality, were also hypothesized by Hornocker (1969) to regulate numbers of mountain lions in a given area. Logan et al. (1996) indicated males may also be the chief internal regulation mechanism by direct killing of conspecifics.

Maximum annual survival rates of cubs were reported as 71% in New Mexico (Logan et al. 1996), 67% in Utah (Lindzey et al. 1989), and over 97%

in Alberta (Ross and Jalkotzy 1992). The latter researchers, however, included several litters that were not detected until 6 months of age, the time when most neonatal mortality has already occurred.

Risks associated with dispersal lead to lower survival in subadults than other age classes. Male subadults probably have lower survival rates than females. Logan et al. (1996) provide the only study to assess accurately gender-specific subadult survival. They estimated a 56% survival rate for males and 88% for females in New Mexico. Anderson et al. (1992) calculated a pooled survival rate of 64% for mountain lion aged 12-24 months in Colorado. Their pooled rate is very similar to that reported by Logan et al. (1996) if their gender rates are pooled. Estimates of subadult survival rates from other studies is lacking.

Logan et al. (1996) found that adult males had higher annual survival rates (90%) and lived longer than adult females (81% annual survival rate). Lindzey et al. (1988) calculated adult female survival rates of between 45 and 100%, with a mean of 71% using MICROMORT. A combined adult survival rate of 75% was calculated by Beier and Barrett (1993) for a mountain lion population that occupied fragmented habitats in southern California. Anderson et al. (1992) calculated combined adult survival rates of 69%, 92%, and 80 % for mountain lions 24-36 months, 36-48 months, and 48-60 months, respectively in Colorado.

Human-related mortality is generally additive to accidental mortalities, but compensatory to deaths from conspecifics (Lindzey 1987:659). Compensation for mortality is primarily through immigration of transient lions into vacant, non-contested home ranges (Seidensticker et al. 1973, Logan et al.

1986, Sweanor et al. 1996). Female cubs also contribute to population growth by establishment of home areas near or adjacent to their maternal home areas.

Dispersal of subadult mountain lions from their natal areas is an important component of population dynamics in mountain lions (Seidensticker et al. 1973, Logan et al. 1986, Logan et al. 1996). Dispersal may be an evolutionary adaptation to minimize inbreeding, avoid competition for food and space, and a mechanism that insures efficient colonization of new habitat (Sweanor et al. 1996). As much as 30% of a population may be comprised of transient mountain lions. This transient component of the population has been described as a delayed addition to the population (Seidensticker et al. 1973).

Dispersal of subadult males appears independent of population density (Hemker et al. 1984, Logan et al. 1996). Females are less likely than males to disperse and more likely to establish a home area near or adjacent to their maternal home areas (Laing and Lindzey 1994, Lindzey et al. 1994, Logan et al. 1996). Immigration tends to equal emigration if a population and its surrounding populations are productive and increasing.

Much of wildlife management is directed toward affecting population growth by manipulation of vital rates within life stages of a species (McCullough and Barrett 1992). One technique to assess the relative importance of the various vital rates is sensitivity analysis of population models (Burgman et al. 1993:98-100). The importance of each life stage is measured by successively changing each vital rate and measuring the subsequent change in r_0 of a modeled population. A more analytical approach is to calculate elasticity (E) of the finite rate of increase (λ). A population has a positive growth rate when λ is greater than 1.0 and a negative growth rate when λ is less than 1.0. Elasticity is defined as the proportional change in λ with proportional

changes in vital rates (Caswell 1989). The higher the elasticity of a vital rate, the greater the effect on λ . Sensitivity studies encourage the best investment of conservation dollars by focusing management action on the most important vital rates in a population or species (Goodman 1980). The utility of sensitivity analysis is exemplified in a variety of vertebrates such as fish (Marchall and Crowder 1996), reptiles (Crowder et al. 1994), birds (Heppell et al. 1994), and mammals (Escos et al. 1994).

Wisdom and Mills (1997) provided a technique to further define and quantify the relative importance of each vital rate. They regressed λ on the value of each vital rate across 1,000 replicates and calculated a coefficient of determination (r^2) for each parameter. Values of r^2 permit a direct comparison of the magnitude of the effect on λ when vital rates vary simultaneously and disproportionately.

METHODS

To assess lion management I developed a stochastic population model based on the life history of mountain lions. Key assumptions of the model were that environmental resources were unlimited and immigration equaled emigration. Both assumptions are seldom true in natural systems. However, indices of mountain lion abundance in Montana suggest recent growth in the lion population has been nearly exponential (Riley Chapter 3 this ms). The second assumption is also less likely to be violated when populations are increasing.

Model Construction

The annual life cycle of the simulated lion population is described by a simple birth and death model (Figure 4.1). The annual cycle begins with the population at its lowest level in late winter just before the breeding season. Breeding occurs in spring and births follow in a summer season. Adult mortality occurs during a harvest season that normally occurs in late fall or early winter. Sex ratios of subadults in the model are adjusted just before recruitment. A separate nested model was constructed for each life stage process depicted as ellipses and arrows.

I evaluated the model's behavior and correspondence to real system data from a New Mexico study provided by Logan et al. (1996). The model was initiated with population parameters observed during their initial years of study. A 10-year time span was then simulated for 50 runs of the model. Mean estimates for each parameter from the model population were then compared with the observed estimates. Slight tuning of the model was made and another iteration run. All model outputs were within $\pm 10\%$ of the observed estimates.

To parameterize the test model, I gathered demographic data about mountain lions from reports of field studies across western North America (Table 4.1). These values were collected under a broad range of geographical and ecological conditions as well as different sampling techniques. Thus, the values may contain both sampling error and variation due to environmental effects. However, I assumed that the estimates depicted the range of plausible vital rates among mountain lion populations. Values for the 5 vital rates were programmed to vary randomly between the values displayed in Table 4.1. All other values were set based upon mean values from previous research.

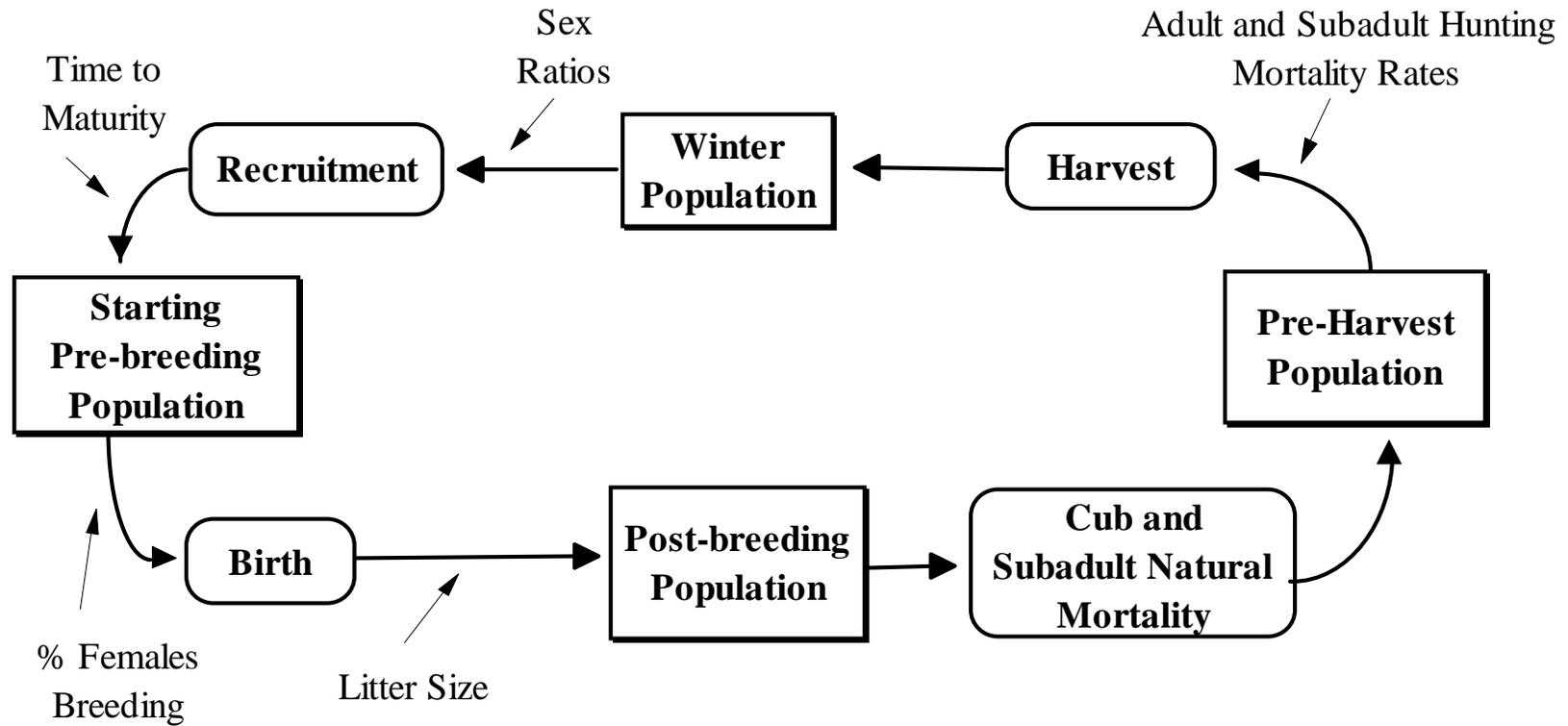


Figure 4.1. The annual life cycle of mountain lions in Montana as depicted in a stochastic birth and death population.

Table 4.1. Population characteristics of mountain lions from selected studies in North America.

<i>Source</i>	<i>Litter Size</i>	<i>Kitten Survival</i>	<i>Sub - Adult Survival</i>	<i>Age of First Reproduction (months)</i>	<i>Percent Females Breeding</i>	<i>Ad Female Survival Rate</i>	<i>Ad Male Survival Rate</i>	<i>Adult¹ Sex Ratios</i>
Logan et al. 1996	3.0	0.73	0.56 M 0.88 F	26	73	0.81	0.90	1M:1.4F
Spreadbury 1996	3.1							
Lindzey et al. 1994				26	71	0.73	0.72	
Beier & Bennett 1993					75			
Anderson 1992			0.64		69 - 80			
Hornocker et al. 1992	3.2							
Ross & Jalkotzy 1992	2.2				42			
Lindzey et al. 1988					71			
Logan et al. 1986	2.9							
Logan 1983					71			
Hemker 1982					50			
Hornocker 1970	2.6							
Means ²	3.0	0.73	0.70	26	70	0.85	0.85	1M:1.4F

¹ Sex ratios in population model set as subadults are recruited into the population.² Means were weighted calculated from researchers original samples.

The model was simplified for optimization in several ways. First, the model assumed a birth pulse instead of year-round breeding. Despite the ability to breed anytime, nearly 75% of mountain lion births in northern latitudes occur during summer or early fall, and function as a seasonal birth pulse (Anderson 1983 , Logan et al. 1996). Second, male and female survival rates were pooled to form a single age class rate. Only 2 studies (Lindzey et al. 1994, Logan et al. 1996) reported reliable gender-specific survival rates, and because those are both from desert ecosystems they may not be representative of northern populations. Sex ratio at birth was assumed 50:50, but the sex ratio at recruitment was set at 60% females to approximate lower survival rates consistently reported for male subadults (Hornocker et al. 1970, Logan et al. 1986, Beier and Barrett 1993, Ross and Jalkotzy 1992, Lindzey et al. 1994, and Logan et al. 1996). Individuals were considered cubs until 12 months of age and animals > 22 months were considered adults (Logan et al. 1996).

Model process and sensitivity analysis

I conducted a sensitivity analysis and a regression analysis on the effects of varied vital rates. The 2 different tests required a slightly different approach. To determine values of elasticity, I incrementally changed 5 test vital rates (adult survival, subadult survival, cub survival, litter size, and age of first reproduction) by 1% and measured the proportional change in λ (Crowder et al. 1994). The population rate of increase (r_o) was obtained from the slope of a log-linear regression between time and population size for each run of the model; λ was in turn computed from the rate of increase. Elasticity (E) was estimated for changes in vital rate x by the following formula (Crowder et al. 1994):

$$E = (\lambda_{(x + 0.01x)} - \lambda_{(x - 0.01x)}) / (0.02 \times \lambda)$$

To generate data for regression analyses, I varied the 5 parameters randomly within the respective ranges displayed in Table 4.1 for each of 1,000 runs of the model. A uniform distribution was used in randomization to test all plausible combinations of vital rates. A reference λ , used for comparison to the randomized runs, was determined using the mean rates reported in the literature to parameterize the model. I calculated r^2 values using simple linear regression (MINITAB PROC REGRESS, MINITAB, Inc 1996).

RESULTS

The observed reference λ , with all parameters fixed at mean rates, was 1.12. For comparison, a mean $\lambda = 1.09$ (Range 0.90-1.25) was calculated for the 1,000 stochastic runs of the model (Figure 4.2). Highest sensitivity was associated with adult survival rates ($E = 0.46$) followed by subadult survival ($E = 0.24$), and cub survival ($E = 0.16$). Changes in litter size ($E = 0.07$) and age of first reproduction ($E = 0.01$) had minor effects on λ .

Regression analyses indicated that adult survival accounted for the greatest variation in λ (Figure 4.3). There was agreement between the measures of elasticity and the regression analysis with respect to ranking the importance of survival rates to λ . However, age of first reproduction and litter size accounted for more variation of λ than did either cub or subadult survivorship.

The lowest adult survivorship associated with $\lambda > 1.0$ was 0.69. The associated values for other vital rates were subadult survivorship (0.87), cub survivorship (0.71), litter size (3.15), and age of first reproduction (2.83). The highest adult survivorship associated with $\lambda < 1.0$ was 0.95, where subadult

survivorship was 0.69, cub survivorship 0.52, litter size 2.49, and age of first reproduction 2.31.

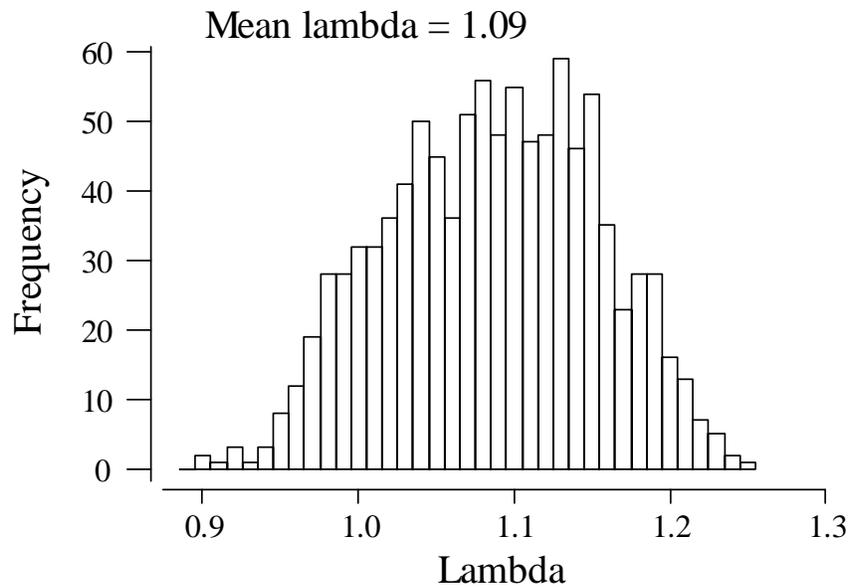
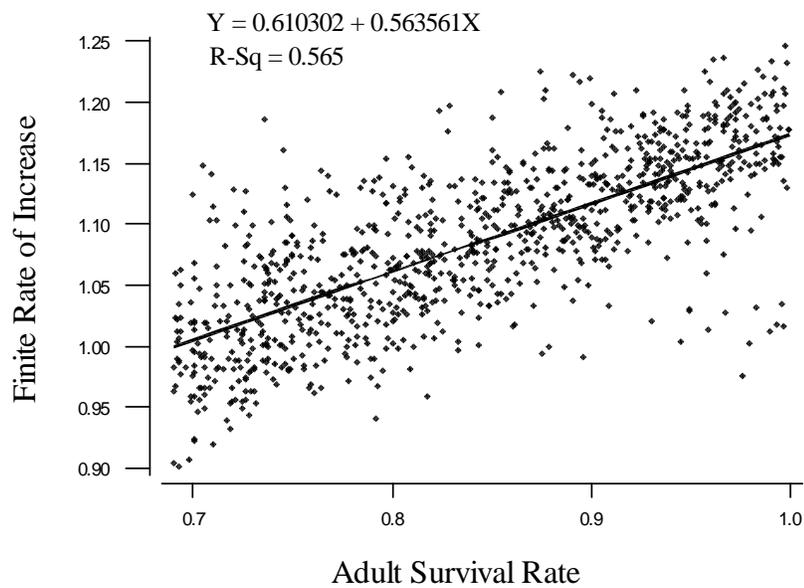


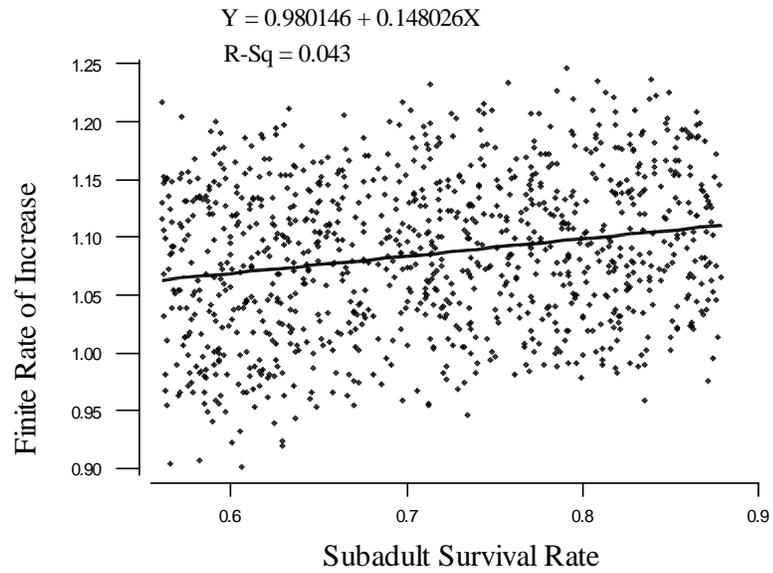
Figure 4.2. The distribution and range of the finite rate of increase (λ) for mountain lions based upon 1,000 replicates of a stage-structured population model. Values for stage-specific survival rates, litter size, and age of first reproduction were randomly selected from a uniform distribution within bounds established from field studies (Table 4.1).



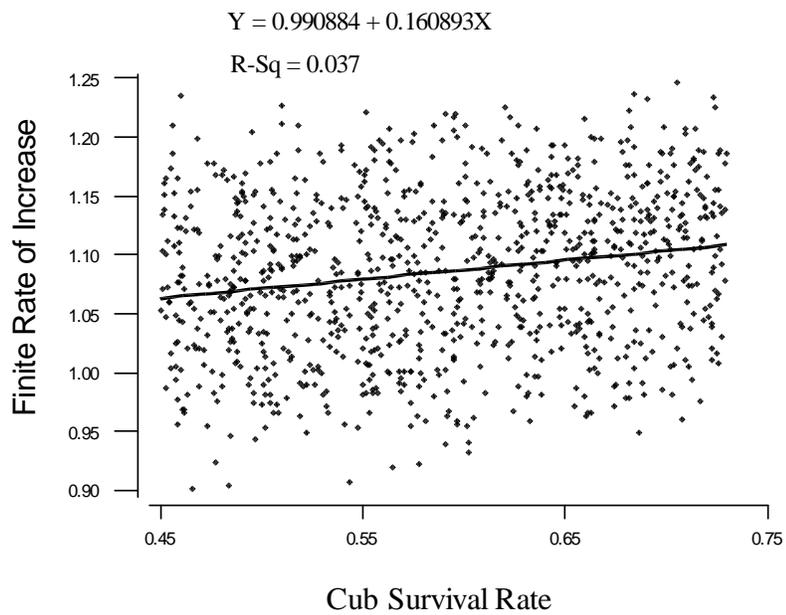
a)

Figure 4.3. Regression analyses of a) adult survival rates, b) subadult survival rates, c) juvenile survival rates, d) litter size, and e) age of first reproduction on the finite rate of increase for mountain lions based upon 1,000 replicates of a stage-structured population model. Vital rates were randomly selected from a uniform distribution within bounds established from field studies (Table 4.1).

Figure 4.3 (Continued)

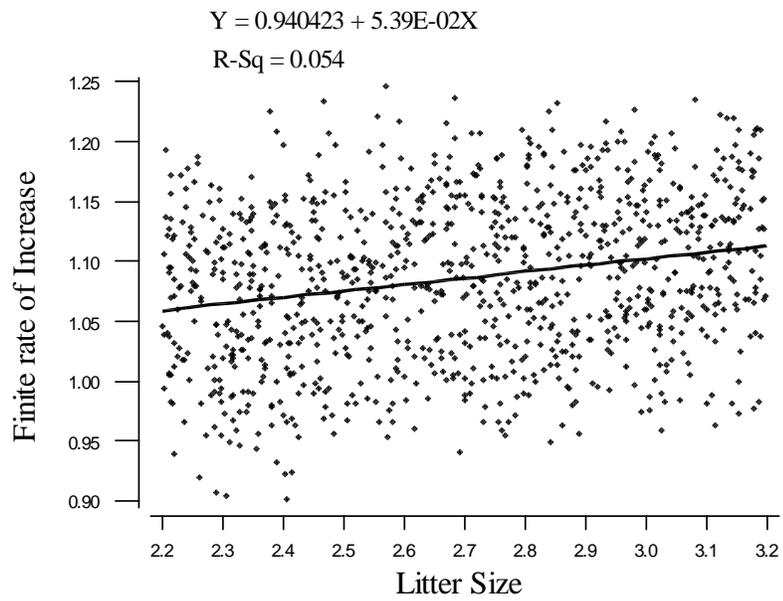


b)

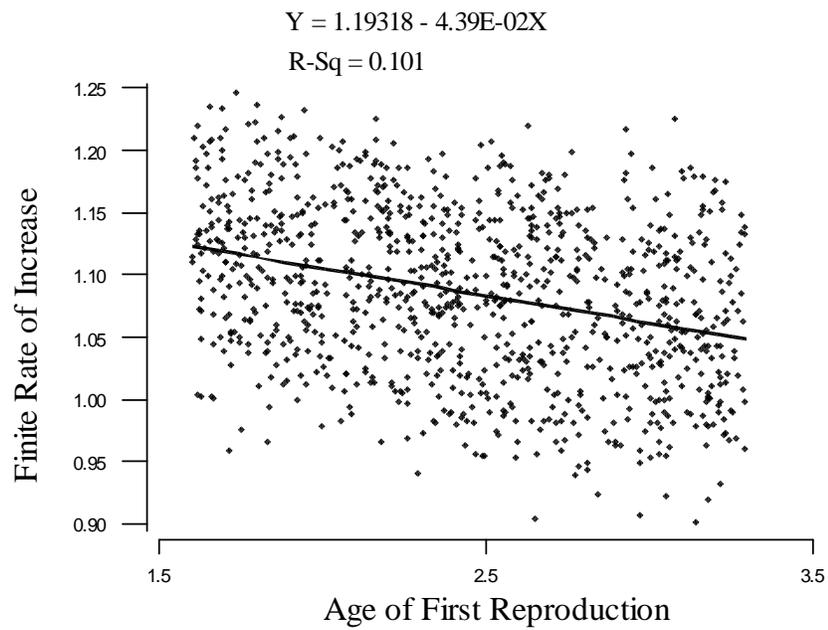


c)

Figure 4.3 (Continued)



d)



e)

DISCUSSION

When all variables were set to mean values derived from the literature, the estimate of λ from the model was consistent with values of λ reported from most field studies, but less than the maximum ($\lambda = 1.49$) reported under optimal conditions (Tanner 1975). Logan et al. (1996) calculated λ values of 1.21 and 1.28 for the San Andres Mountains mountain lion population during 2 different time periods. However, these researchers also observed annual λ values as low as 1.05 in the same population after protection from human-caused mortality. Logan et al. (1996) hypothesized that the study population was approaching carrying capacity for existing habitat conditions. Logan et al. (1996) also calculated λ from 2 other studies (Ross and Jalkotzy 1992, Lindzey et al. 1994) and found λ values that ranged from 1.04 to 1.08 for an Alberta population, and $\lambda = 1.24$ over a 5 years in a protected Utah mountain lion population. Based upon model outputs, all these reported rates span the range of λ values expected under high-to-very high subadult and adult survival.

The broad distribution displayed in the regression of λ and vital rates is primarily due to variation programmed in for a hypothetical situation. The importance that any specific vital rate has in affecting λ is expected to vary with the underlying probability distribution of values for the other vital rates and the covariance of the values among the various life stages (Caswell 1989). For mountain lions in most natural settings, the level of variation in vital rates probably does not approach that in the model populations, especially over small time spans. The model does, however, demonstrate the array of plausible variation that could be expected over longer spatial scales.

My results emphasize that r_0 for mountain lions is sensitive to small changes in adult survival rates, and support findings from field studies by Logan et al. (1996) and Lindzey et al. (1994). Considerable correlation between the model's outputs and those of the limited empirical studies is expected because vital rates used in the model were partially derived from those field studies. The results from empirical studies and outputs of the model imply that adult survival must be at least 65% to promote positive population growth in mountain lions. If survival rates in other age classes are lower or litter sizes are less than average, adult survivorship must be higher to promote growth in a population.

The significant effect that adult survival rates have on λ has been found in numerous other studies of long-lived species such as Everglade Kites (Nichols et al. 1980), black rhinoceros (Conway and Goodman 1989), and African lions (Starfield et al. 1981). Demetrius (1969) predicted early on that small increases in survival would have much greater effects than increased fecundity. That assertion is also supported by my model of mountain lion population dynamics.

From a conservation perspective, it is fortuitous that adult survivorship has the greatest effect on λ since that is the vital rate most easily affected by management. Mountain lion population management generally involves hunting that targets adult lions. Hunting season structure and harvest quotas that result in higher adult mortality have the potential to greatly affect λ of mountain lion populations. However, the relatively high r_m expressed by mountain lions indicates their capacity to rapidly rebound from a decrease in numbers. Results from field studies, where habitats were not greatly perturbed,

support this assertion (Ross and Jalkotzy 1992, Lindzey et al. 1994, Logan et al. 1996).

Animal damage control is another commonly used population management technique. Contrary to hunting, animal damage control most often affects subadult mountain lions, the life stage most likely to cause problems (Riley and Aune 1996). Based on outputs from the model, such damage control measures are predicted to affect the offending individual animal, but probably do little to affect the overall growth rate of a population.

My results suggest that compensation for high adult mortality is not probable within a population. Litter sizes are not expected to vary appreciably because they have been set as an evolutionary strategy that optimizes the trade-off between maternal fitness and maximum contribution of genetic material to a population. Compensation from within the population must then come from either improved kitten survival or reduced age of first reproduction. However, neither variable appears to play a significant role in population growth. Additional recruitment must come from outside the population, most likely in the form of dispersing subadults as suggested by Seidensticker et al. (1973), Lindzey et al. (1994) and Logan et al. (1996).

Disagreement among ranking of vital rates between analyses of elasticity and regressions is partially due to different scales at which the rates vary through time. The survival rates are directly comparable because they are on the same scale. Litter size and age of first reproduction vary across a more widely disparate distribution than survival rates or each other. Whereas adult survivorship remains the overarching parameter that affects λ , environmental changes that could alter age of first reproduction, such as available habitat for new territories, could significantly influence variation in r_0 .

Modeling vividly depicts the numerical importance of various life stages. However, it is worthwhile to keep in mind that populations are comprised of individual animals in a real world, with unique behaviors and may contribute more or less than a $1/n$ value to the population (Caughley 1977:2). Seidensticker et al. (1973) and Sweanor et al. (1996) emphasized the important role that certain adults may play in mountain lion social organization. A majority of the offspring that survived to recruitment age were from a minority of females. Seidensticker et al. (1973) warned that subadult mountain lions should not be viewed merely as a vulnerable surplus to a population. Dispersal by subadults promotes efficient colonization of unfilled home areas, enhances genetic outcrossing, and increases the probability that isolated populations will not suffer from inbreeding or other extinction risks (Sweanor 1990). The territorial behavior and subsequent land tenure system of adults is hypothesized as the mechanism that regulates r_m on a landscape (Logan et al. 1996). These important demographic features of mountain lions are potentially masked in a sensitivity analysis such as the one described in this paper.

Nonetheless, opportunities to collect accurate field estimates of population vital rates on mountain lions are infrequent and very costly. The obstacles may be insurmountable for most wildlife managers, given multiple priorities and inadequate budgets typical of most wildlife management situations. In these situations, models provide guidance for constructively thinking about populations and furnish valuable insights into mechanisms of growth in populations (Starfield 1997). The results of my model suggest that efforts should focus on obtaining measurements of adult survival. Lower priorities should be given to the collection of vital rates such as litter size, age of first reproduction, and cub survival. Even when efforts can be made to

collect estimates of vital rates, measurement error is likely to be great due to the secretive behavior of mountain lions and small sample sizes associated with the relatively low densities at which lions occur.

MANAGEMENT IMPLICATIONS

Litvaitis et al. (1996) suggested that there are temporal and spatial scales to the management of felids. In the short term, managers can most affect population growth of mountain lions by regulating adult survival. Long-term management actions such as changes in environmental productivity (Riley, Chapter 3 this ms) could be expected to affect cub and subadult survival, and possibly lower the age of first reproduction. Nonetheless, none of these variables can be expected to have the effect on population growth over the short term that will occur from changes in adult survival.

The importance of adult survival to mountain lion demographics is fortunate because many management practices such as hunting or animal damage control already target survival of adults. If the goal is to maintain or increase populations, managers must be sensitive to the rate of adult harvest; populations cannot fully compensate from within the population for excessive harvest.

Models should not be a substitute for empirical field investigations (Bunnell and Tait 1980). However, models can afford important avenues that lead to better understanding of population dynamics for species that are difficult to census or when the dynamics of a system are poorly understood (Starfield 1997). Because mountain lions are so difficult to accurately census, mountain lion management in the foreseeable future will likely suffer from inadequate empirical data on vital rates of a population. This paper presents a

first approximation of a mountain lion population model that provides guidance for decisions about population management in the absence of such data.

CHAPTER FIVE

FACTORS THAT AFFECT STAKEHOLDER PREFERENCES FOR MOUNTAIN LION (*PUMA CONCOLOR*) POPULATIONS IN MONTANA.

INTRODUCTION

Recent increases in mountain lion (*Puma concolor*) populations throughout western North America challenge wildlife managers who attempt to balance the beneficial and detrimental aspects of a large carnivore in human-dominated environments. Concern for the welfare of large carnivores throughout North America has increased as has public desire to restore their role in western ecosystems (Kellert 1985, Noss et al. 1996). Concurrently, agricultural interests express concern about mountain lion depredation on their livestock, hunters worry about the effect of large predators on game populations, and homeowners are finding a new threat to their pets and occasionally themselves.

More than any other factor, the increased frequency of mountain lion attacks on humans and their pets during the past 2 decades (Beier 1991, Riley and Aune 1996) elevated lion management to a national issue (Stevens 1994). The issue is likely to remain significant as the West undergoes the most drastic redistribution of human populations since the early land rush days of the late-1800s (Riebsame 1997). Of the 10 US states with the fastest growing human populations during the 1990s, 8 support stable or increasing populations of mountain lions (Padley 1997).

Opportunities to influence wildlife acceptance capacity (WAC) provide additional management strategies in addition to direct manipulation of mountain lion populations. Wildlife acceptance capacity is a concept adapted from biological carrying capacity and is an estimate of the maximum numbers

of a wildlife species that is acceptable to people in an area (Decker and Purdy 1988). Wildlife acceptance capacity is based on stakeholders' perceptions rather than a biological estimate of populations in relation to their habitat. Stakeholders demonstrate a hierarchy of tolerance to problems caused by wildlife (Decker 1994). The proposed hierarchy predicts acceptance is less for animals that pose a perceived risk to human health and safety than for those that threaten only economic damages. The acceptance of monetary losses, in turn, is less than the endurance for general nuisances or diminishment of esthetic values.

Acceptance levels of wildlife are also expected to vary with situations and the stakeholders involved. Factors identified as important determinants of WAC include stakeholder experience with wildlife; esthetic values and attitudes toward the referent species; economic condition of the stakeholder; type, amount, and severity of damage caused by the referent species; ability to withstand economic impacts from damage; perceptions of population trends; and, attitudes towards management (Decker and Purdy 1988, Craven et al. 1992). Tolerance among a particular stakeholder group generally decreases as damage increases (Pomerantz et al. 1986, Seimer and Decker 1991), but stakeholders with similar levels of economic loss often express dissimilar levels of damage tolerance. Ultimately, tolerance levels depend upon perceptions of what is at stake, that are in turn dependent upon stakeholders' attitudes, beliefs, knowledge, and experiences (Decker 1994). To influence public perceptions toward mountain lions management needs to better understand what factors influence stakeholders' underlying beliefs and attitudes towards the species.

From a conservation standpoint, management of acceptance capacity for mountain lions may be a necessary supplement to direct population control.

Several states recently have lost opportunities to hunt mountain lions through voter referendums that were costly from political as well as economical perspectives (Gill 1996). New approaches to communication with all stakeholders, and accurate assessment of the perceptions and preferences of all stakeholders are required if wildlife professionals are to maintain a central role in socially responsive conservation (Knuth et al. 1992, Decker et al. 1996, Manfredo et al. 1998).

Traditional interactions with stakeholders, such as public meetings and reaction to management proposals, seldom contribute constructively to policy formation (deLeon 1994). One serious shortcoming is the general lack of detailed information acquired regarding factors that affect people's acceptance of wildlife. Significant discrepancies between agency goals and stakeholder population preferences can lead to erosion of trust in government and initiate political repercussions for the management agency (Slovic 1993).

Significant gains in knowledge about mountain lion ecology have occurred since 1960 (Anderson 1983, Lindzey 1987, Logan et al. 1996). Most approaches to carnivore conservation have been based in ecology (Noss et al. 1996). However, success of efforts to conserve large carnivores depend as much on social acceptance by regional publics as on understanding biological variables (Kellert et al. 1996, Fuller and Kittredge 1996). Durable solutions to any conservation problem require integration of human dimensions considerations with ecological dimensions (Pickett and McDonald 1993).

My objective was to make an initial inquiry into stakeholders' beliefs and attitudes toward mountain lions, and determine factors that affect stakeholder preferences for mountain lion population trends in Montana. I report data collected across diverse ecological and socioeconomic landscapes

that reflect a range of mountain lion densities from relatively high in northwestern Montana to rare or nonexistent in the eastern portion of the state (Chapter 3, this ms). Implications focus on the relevance of my findings for environmental and risk communication that provide an avenue for affecting society's acceptance capacity for mountain lions. The applicability of these findings to conservation of other large carnivores is discussed.

LITERATURE REVIEW

Contemporary approaches to solving environmental problems are heavily weighted toward ecological investigations. However, a recognition of the imperfect nature of knowledge gained from ecological investigations (Shrader-Frechette 1994) will shift the responsibility for conservation action away from ecologists and into economic and social arenas (Jordan and Miller 1996). Socioeconomic considerations will then have a greater role in wildlife management. Application of social science theory can make wildlife management a much more comprehensive discipline (Decker et al. 1992). However, systematic human dimensions inquiries designed to help guide wildlife management, particularly for rarely studied species such as mountain lions, are currently inadequate.

The research record on stakeholder knowledge, beliefs, and attitudes towards carnivores such as mountain lions is negligible. Knowledge of societal aspects must be gleaned from contemporary theory derived for other groups of species. Inferences about human dimension considerations of large carnivores have focused on studies related to wolves or grizzly bears (Kellert et al. 1996).

Kellert (1983) asserted the variables that most likely influenced public attitudes towards wildlife conservation were aesthetic value of a species,

phylogenetic relation (similarity) of the species to human beings, presumed threat of the species to human health and productivity, cultural importance, and perceived or actual economic value associated with a particular species.

Mountain lions have attributes that potentially create discordance in attitude formation. Mountain lions simultaneously possess features that many stakeholders may find both desirable and undesirable. For some people living in the West, mountain lions may be an admired large predator, but may also present real or perceived safety and economic threats.

Attitudes are typically positive towards the largest, most adorable animals that are perceived to be safe. Nonconsumptive users of wildlife even express a preference for large, well advertised species (Fazio and Belli 1977). In a broad, national study, Kellert and Berry (1981) found people across all attitudinal alignments expressed the most favorable attitudes towards pets and large animals such as elephants and bears. The least favorable attitudes were expressed towards biting-stinging insects and animals perceived to cause human injury or disease.

Large carnivores hold special meanings for many indigenous cultures, yet represent evil to many of the cultures introduced to this continent (Bolgiano 1995). Despite their ability to threaten humans, pets, and livestock, however, mountain lions assume much less prominence in native North American human culture than either the wolf (Lopez 1978) or the grizzly bear (Kellert et al. 1996). Their solitary and secretive behavior are explanations offered for why the mountain lion has not played a greater role in human cultures native to North America (Kellert et al. 1996). European and Asian immigrants to North America brought a history of interaction with wolves and bears, species present in those areas. Many of the early beliefs about mountain lions were founded in

explorer's knowledge of African lions (Young and Goldman 1946). Mountain lions, indigenous only to the western hemisphere, are a relatively new species to those cultures.

Knowledge is generally an important cognitive component of attitude formation (Eagly and Chaiken 1993). Kellert and Berry (1981) found that Americans were most knowledgeable about animals that inflict injury and disease to humans. Whereas the general public was found to be relatively uninformed about environmental issues as a whole, people were most informed about those issues involving threats to human health and safety. Attitudes towards wolf reintroduction in Colorado were based more on values and emotions than on knowledge (Bright and Manfredi 1996). A lack of knowledge of wolf-human relationships translated into fear of the unknown among stakeholders in the North Fork of the Flathead, Montana (Tucker and Pletscher 1989), as it did in Michigan (Hook and Robinson 1982).

Kellert (1985) reported a trend of more favorable attitudes towards predators with increased urbanization. This may reflect little actual experience with predators on behalf of urban residents. In a Colorado study (Zinn and Manfredi 1996), no significant difference regarding fear of lions was detected between Denver Metro and Front Range foothills residents. However, many of the foothill residents were recent immigrants from the Metro area or commuters to urban areas; perhaps those stakeholders lacked first-hand experience with mountain lions.

One finding consistent in all studies is that livestock producers and rural landowners have the least favorable attitudes towards large carnivores of any demographic group (Kellert 1985, 1987, Thompson 1992, Tucker and Pletscher 1989, Bath and Buchanan 1989). Livestock producers in Alberta were willing

to tolerate low levels of wolf predation on cattle, but quickly became unsympathetic towards wolves when damage exceeded approximately 2% of their herds (Bjorge and Gunson 1983). Attitudes among livestock producers became disfavorable regardless whether they were compensated for full market value of the their losses.

Llewlynn (1978) reported a positive relationship between attitudes towards wolves and distance from a reintroduction site. This conflicts with Kellert's (1985) findings that Alaskans had the most positive attitudes toward wolves of any geographic group in the US. I hypothesize the discrepancy may be due to definition of what is at stake and the difference between perception and reality. Both Llewlynn (1978) and Bath and Buchannan (1989) were working with hypothetical reintroduction of wolves to areas where they had been extirpated for at least 75 years. Local stakeholders in their studies were responding to their emotions and perceptions, not first-hand knowledge. Alaskans, however, have considerable exposure to real-life experience with wolves and may perceive that wolves really do not pose enough threat to human welfare to make them an overarching concern. The perceived risk to economics or human safety apparently did not exceed the perceived esthetic values of wolves. Livestock is not an issue in Alaska. However, when competition for moose is a concern, Alaskans' support wolf control actions (Gassaway et al. 1983).

Research into risk perceptions may help elucidate attitude formation related to carnivores that have a record of harming humans. Risk is generally defined as the chance or possibility of suffering harm or loss involving uncertain hazards or dangers (Renn 1992). Studies of risk grew out of the practical needs of industrialized societies to regulate technologies (Slovic et al.

1981), and the desire to protect themselves from natural and human-caused hazards. Humans have thought about risk for more than a millennia to make sense out of the inherent uncertainties of nature (Bernstein 1996). However, risk studies are only now being incorporated into modern natural resource management (Knuth et al. 1992).

Wildlife acceptance capacity is a concept adapted from biological carrying capacity and is an estimate of the numbers of a wildlife species in an area that is acceptable to people (Decker and Purdy 1988). Wildlife acceptance capacity is based on stakeholders' perceptions rather than biological estimates of a population in relation to its habitat. Stakeholders seem to demonstrate a hierarchy of tolerance to problems caused by wildlife (Decker 1994). The hierarchy predicts acceptance is less for animals or situations that pose a risk to human health and safety than for those that threaten only economic damages. The acceptance of monetary loss, in turn, is less than for general nuisances or loss of esthetic values.

Acceptance levels of damage caused by wildlife are expected to vary with upon situations and the stakeholders involved. Factors identified as important determinants of acceptance/tolerance include type, amount, and severity of damage, ability to withstand economic impacts from damage, attitudes towards the species involved, perceptions of population trends, and attitudes towards management (Craven et al. 1992). Tolerance generally decreases as damage increases (Pomerantz et al. 1986, Seimer et al 1991), but people with similar levels of economic loss often express dissimilar levels of damage tolerance. Ultimately, tolerance levels depend upon perceptions of what is at stake, that are in turn dependent upon stakeholders' attitudes, beliefs, knowledge and experiences (Decker 1994). Other attributes may include a

stakeholder's experience with wildlife, the esthetics value of the referent species, the economic condition of the stakeholder, the economic dependency of the stakeholder on the resource being threatened, and attitude of stakeholder towards management (Decker and Purdy 1988, Craven et al. 1992).

METHODS

I conducted personal interviews during fall 1996 to determine salient issues and local vernacular associated with mountain lions in Montana. Interviews were held with 34 individuals who reflected at least 10 different relationships to mountain lions. Stakeholder interests represented were: people who had personal confrontations with a mountain lion (n = 3); urban (n = 5), suburban (n = 5), and rural homeowners (n = 5); cattle (n = 2), sheep (n = 3), and llama growers (n = 2); deer hunters (n = 5); carnivore welfare activists (n = 1); and animal damage control officers (n = 3). I also conducted a nominal group meeting (Moore 1987) with 13 wildlife managers who represented all geographical areas of Montana. The moderated meeting was conducted to determine managers' perceptions of the most important factors that affect stakeholder preferences for mountain lion populations in their respective regions. The primary purpose of the interviews and nominal group meeting was to help guide development of a questionnaire that could enable quantitative descriptions of stakeholders and an analysis of factors that affect their preferences for mountain lion populations in Montana.

Questionnaire Development

The mail-back questionnaire contained 13 items focused on 6 primary subject areas: involvement with mountain lions, perceptions of current

population trends, attitudes towards mountain lions, risk beliefs associated with lions, subjective health/safety risk judgments with regard to lions, and preferences for lion populations in the immediate future (Appendix IV). General questions about wildlife interests and wildlife-related activities preceded specific questions directed toward the primary areas of interest. Questions were also asked at the end to determine geographical setting of each respondent's residence, duration of their Montana residency, livestock ownership, number of children in the household, and age, gender, and level of formal education attained by the respondents.

I assessed involvement with mountain lions by providing 10 potential ways a respondent could have experiences with mountain lions. The series was designed as a continuum of potential experiences that ranged from no experiences, to observation of a mountain lion in the wild, to being personally threatened by a lion or having pets or livestock threatened. Five additional experiences were vicarious in that a respondent only read or heard about lion interactions with pets, livestock or other people. The experiences were classified as a variable, INVOLVE, that had 5 levels: very high (personal threat to self or family member), high (respondent or family member personally had a friend, pet, or livestock threatened), moderate (respondent read/heard about lion-human interactions), low (respondent read/heard about lion management or family member read about a lion-human interaction), and none (no experience with listed items).

I measured respondents' perceptions of current mountain lion population trends and preferences for future population trends on 5-point progressive scales. The scales ranged from decrease(d) greatly to increase(d) greatly. A "don't know" or "no opinion" option was provided on all questions. Variables

were created from perceptions of current mountain lion population trends (CPOP), and preferences for future populations (FPOP).

A variable, ATTITUDE, was derived from a list of 7 belief statements about mountain lions. Respondents were asked to indicate their agreement on a 5-point progressive scale that ranged from disagree strongly to agree strongly. Factor analysis (Kim and Mueller 1978) indicated all 7 statements formed a reliable attitudinal scale.

Risk beliefs were measured with a semantic differential format (Issac and Michael 1981:144) of adjective pairs as endpoints on a 5-point scale. The 7 adjective pairs were derived from previous risk studies (Slovic 1987), but modified for relevance to mountain lions. Factor analysis indicated 2 reliable factors: perceptions of current trends in potential risks from mountain lions (RTREND), and beliefs related to risks (RBELIEF) such as levels of dread, ability to live with the risks, equality of risks, voluntariness of risk acceptance, and how well science understands the potential risks to humans from mountain lions.

A risk ladder was used to measure subjective judgments about the level of risks posed to human safety from mountain lions. The ladder was a logarithmic scale with 26 steps for respondents to choose from along the left side that ranged from 0:10⁶ to 10⁶: 10⁶ chances of death from mountain lions. Objective estimates were displayed on the right side of the ladder, along with a comparison to familiar risks such as commercial airline accidents, automobile accidents in Montana, and at the extreme, climbing Mt. Everest.

Questionnaire Administration

I used a self-administered, 4-wave mail questionnaire that followed guidelines provided by Dillman (1978) and Brown et al. (1989). The first wave of questionnaires was mailed to 500 randomly selected households in each of three strata: western, central, and eastern Montana. The geographical area within each strata coincided with the 3 general Ecoregions (Chapter 3, this ms) identified with different mountain lion densities and different levels of lion-human interactions (Riley and Aune 1997). Approximately 34%, 48%, and 18% of Montana's human population were estimated to live in the western, central, and eastern Montana strata, respectively.

The first-wave mailing occurred 15 February 1997. All questionnaires and correspondence were mailed from and returned to Helena, MT under Montana Fish, Wildlife and Parks letterheads. To assess nonresponse bias, I attempted to telephone all people in the sample who were nonrespondents as of 10 April 1997. Nonrespondents were asked a sample of questions from all the main topic areas for comparison to the respondent sample.

Statistical Procedures

Logistic regression with stepwise variable selection ($p < 0.05$ cutoff value, SPSS Inc. 1990:312) was used to construct a model that best predicted FPOP. Independent variables selected *a priori* were INVOLVE, CPOP, ATTITUDE, RTREND, RBELIEF, and 2 demographic variables, children in household and livestock ownership. A change in likelihood ratio method (Knoke and Burke 1980:30) was used to identify the most parsimonious model.

Chi-square statistics were used for testing differences in proportions between variables, and one-way ANOVA was used to test for differences between multiple means.

RESULTS

Survey Response

Questionnaires were delivered to 1,378 (91.9%) households selected for the sample. Adjusted return rates were 58.4% (n = 268), 57.7% (n = 267), and 59.2% (n = 270) for western, central, and eastern Montana strata, respectively. Results from the nonrespondent telephone survey (n=138) suggested non-respondents were more ambivalent towards mountain lions than respondents. For example, 38%, 50%, and 65% of the nonrespondents in western, central, and eastern Montana strata, respectively, expressed no particular feelings towards lions as compared to 8%, 14%, and 22.6% of the respondents in those respective strata. Nonrespondents were also more likely to answer “don’t know” when asked to describe the current lion population trend, and “remain at current level” when asked for a preferred lion population change in the future. A lower proportion of nonrespondents in western Montana lived in cities of greater than 15,000 people. In central Montana, a lower proportion of the nonrespondents lived in suburbs. Whereas the respondent population was 76.8% male, the non-respondent population was 57.2% male.

My results may therefore be biased toward males, and those people with an interest in lions and with definitive opinions about past and future lion population trends. However, I believe these differences are not so great as to affect hypothesis testing or change the implications of my findings.

Involvement With Wildlife and Mountain Lions

People across Montana were interested in wildlife (95.7%) and active in wildlife-related activities (52.0%, Figure 5.1). Interest and active participation in wildlife-related activities decreased slightly from west to east. Wildlife-related TV programs, videos, or movies were identified as the most common activities that bring people into contact with wildlife (Table 5.1). Reading about wildlife, watching wildlife outdoors, and hiking in the mountains or foothills were activities reported by over half of respondents. Similar to interests, participation in wildlife-related activities diminished from west to east across Montana. Nearly half of respondents indicated they regularly hunt big game. Very few respondents had not participated in any wildlife-related activity listed.

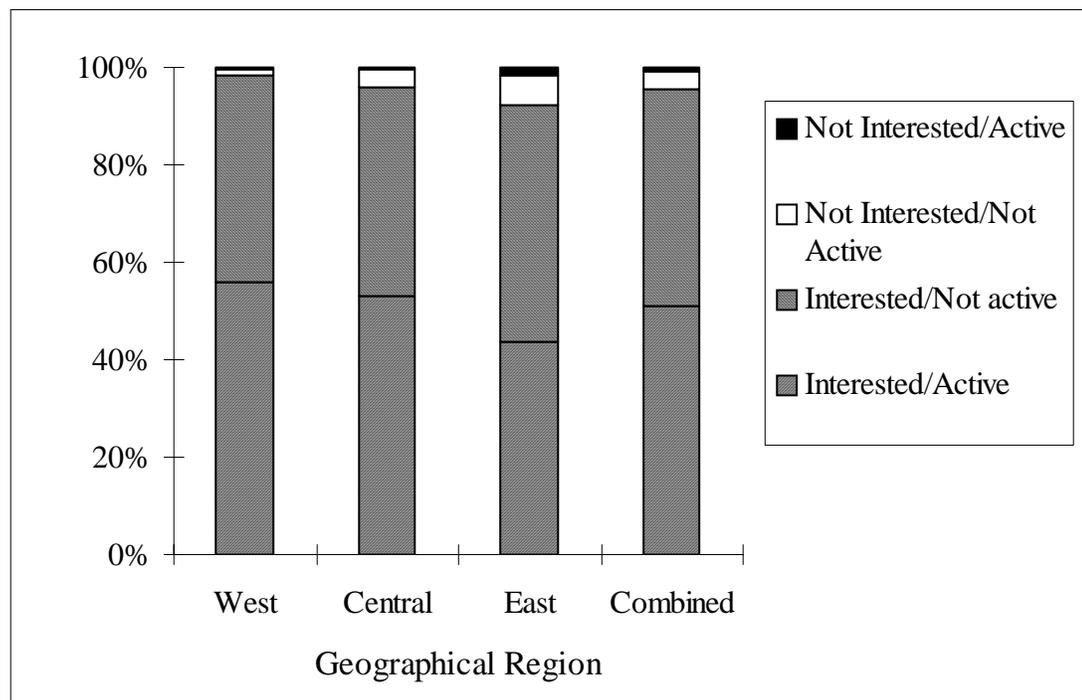


Figure 5.1. Percent of respondents from western, central, and eastern Montana that indicated their interest and participation in wildlife-related activities.

Most respondents (85.6%) were classified as having a medium level of involvement with mountain lions (Figure 5.2). Western Montana had a higher proportion of respondents in the very high category and fewer in the low category than central and eastern Montana.

The most common categories of involvement with mountain lions included reading/hearing about government animal damage control actions, or reading/hearing about encounters between mountain lions, pets, livestock, or people (Table 5.2). Approximately 36.3% of respondents indicated they had observed a mountain lion in the wild, but fewer than 4% reported a threatening

Table 5.1. Percent of questionnaire respondents from west, central and eastern Montana that indicated they participated in various outdoor and wildlife-related activities.

Activity	West	Central	East	Combined
Watch wildlife related TV, videos, or movies.	82.8	81.3	83.3	83.7
Read about wildlife.	75.0	74.5	64.4	72.7
Observe or study wildlife outdoors.	63.8	62.2	50.0	60.0
Hike in the foothills or mountains.	66.0	71.9	34.8	59.0
Hunt big game.	51.5	48.3	45.6	49.3
Mountain bike in the foothills or mountains.	25.0	20.6	4.8	17.2
Work on a farm or ranch.	12.3	15.4	22.6	16.8
Jog in the foothills or mountains.	11.9	12.0	2.6	9.0
Hunt mountain lions.	6.0	5.6	1.1	4.3
None of the above.	2.6	1.9	2.6	2.3

Table 5.2. Percent of questionnaire respondents from west, central and eastern Montana that indicated they had various involvement with mountain lions.

Involvement	West	Central	East	Combined
Observed a mountain lion in the wild.	46.3	40.1	21.0	36.3
Read or heard of mountain lion being killed by authorities.	81.3	73	51.5	70.1
Had a pet threatened or attacked by a mountain lion.	3.7	1.5	0.7	2.0
Had livestock threatened or attacked by a mountain lion.	4.9	3.4	2.6	3.7
Have been personally threatened by a mountain lion.	5.6	3.4	0.7	3.3
Read or heard of pets being threatened/attacked by a mountain lion.	81.7	69.3	50.4	68.4
Read or heard of livestock being threatened/attacked by a mountain lion.	64.2	57.7	55.9	60.4
Read or heard of other people being threatened/attacked by a mountain lion.	79.5	67.4	45.6	65.5
Know a friend/neighbor who had an encounter with a mountain lion.	38.1	28.8	12.2	26.9
None of the above.	3.0	4.5	13.7	6.9

experience. The percentage of people who reported each type of involvement with mountain lions decreased from west to east across Montana. In all cases, response levels from central Montana were intermediate between western and eastern portions of the state. People in western Montana were more than 2x as likely to have observed a mountain lion in the wild, 3 x more likely to know someone who had an encounter with a lion, and over 5 x more likely to have reported being personally threatened by a mountain lion than respondents in eastern Montana. Respondents in eastern Montana were nearly 5 x more likely than those in western Montana to not have any of the different types of involvement listed.

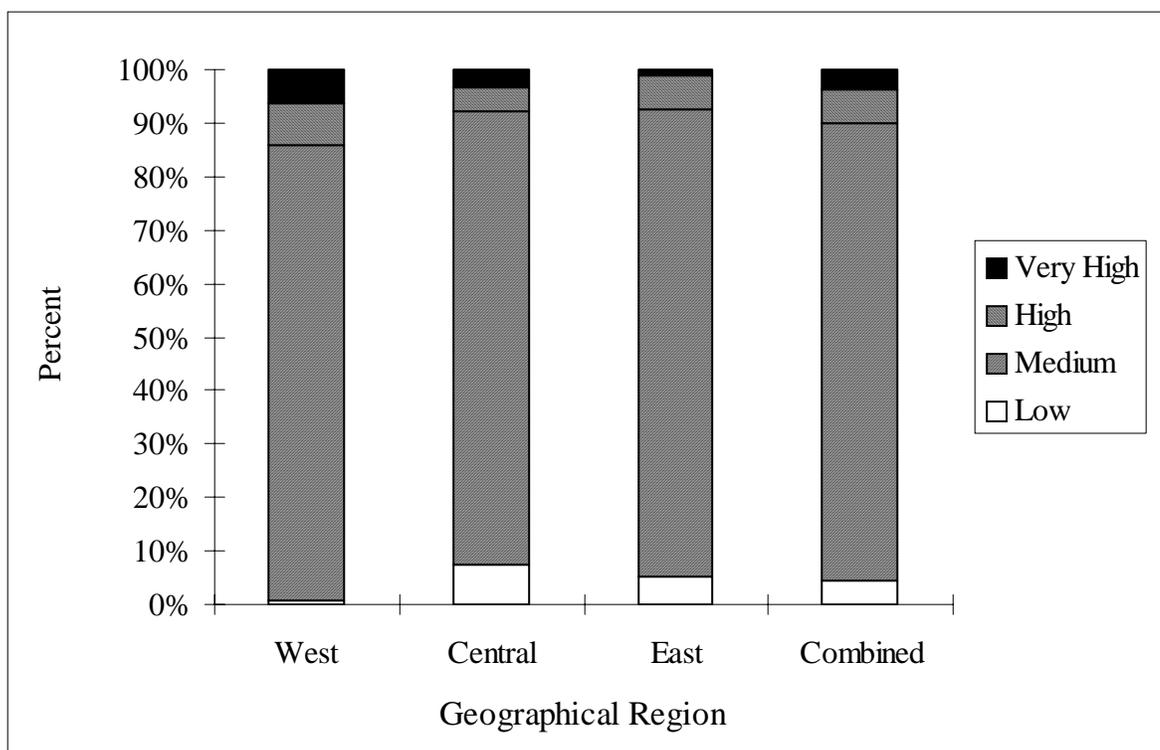


Figure 5.2. Percent of questionnaire respondents from west, central, and eastern Montana with various levels of involvement with mountain lions.

Preferences for Mountain Lion Populations

When asked to express a preference for the mountain lion population trend in their area over the next 5 years, 44.5% of respondents statewide indicated they wanted populations to remain the same (Figure 5.3). Only 12.2% expressed a preference for a larger population while 27.3% preferred fewer mountain lions. The proportion of people who preferred a decrease in the mountain lion population was greatest in the west and least in the east. Conversely, the proportion that preferred the lion population to remain the same, or expressed ambivalence, increased west to east across Montana.

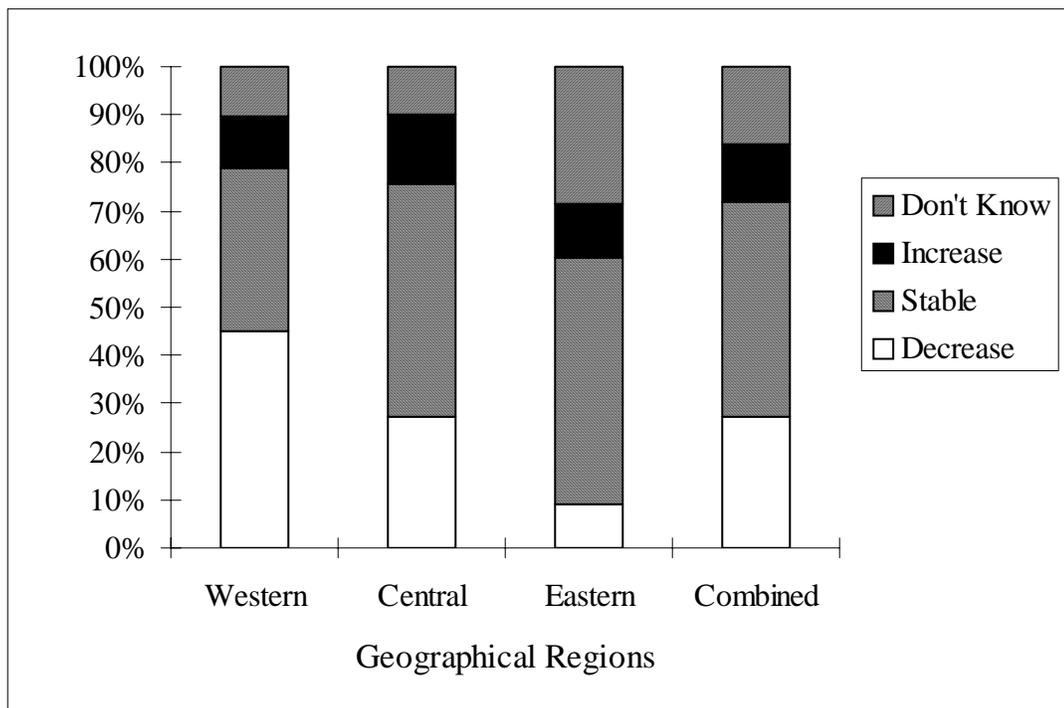


Figure 5.3. The proportion of respondents from western, central, and eastern Montana that expressed preferences for a smaller, no change, or larger mountain lion population in their area of the state.

Statewide, 56.8% of respondents indicated it was important to them personally that the actual mountain lion population trend match their expressed preferences. The importance given to preferred and actual population trends matching was greater in western (65.0% stated it was important) and central Montana (62.2%) than in the east (48.4%). Only 8.4% statewide indicated it was unimportant to them that their preferences were not realized.

Factors Affecting Preferences for Mountain Lion Populations

Three factors, perception of current lion population trend (CPOP), attitudes towards lions (ATTITUDE), and beliefs about risks associated with lions (RBELIEF) formed the most parsimonious model to predict desired future mountain lion population trends (FPOP). The standardized model parameters from logistic regression, in stepwise order (with SE in parentheses), were $\log(P_i)/(1-P_i) = 3.96 (0.62) - 1.33 (0.19) \text{ ATTITUDE} + 2.35 (0.29) \text{ CPOP} - 0.60 (0.17) \text{ RBELIEF}$, where P_i = probability that a respondent will prefer a smaller lion population.

The equation correctly predicted the desired future population trend for 73.8% of the people who chose a smaller and 90.8% of those who chose a larger population or no change in the lion population. Overall, the equation predicted 85.2% of respondents' preference for the mountain lion population trends. People who believed lion populations had increased, expressed negative attitudes towards lions, or believed lions presented a risk to humans had the greatest probability of preferring a decreased population. Demographic variables such as location of residence, livestock ownership, years as a Montana resident, children in household, gender, and level of formal education attained, improved the overall predictive capability of the model by only 0.77%.

My study was not designed to elicit causal factors affecting attitudes or risk beliefs. However, some relationships were apparent (Table 5.3). Whether or not a person was a hunter, INVOLVE, and gender were correlated negatively with perception of current mountain lion populations. Livestock ownership was correlated positively with perceptions of populations. All variables that showed a correlation at $p < 0.05$, except formal educational attainment, were correlated negatively with attitudes and risk beliefs.

Table 5.3. Correlation coefficients of key variables in the model to predict preferences for future mountain lion populations in Montana.

Variable	CPOP	ATTITUDE	RBELIEF
INVOLVE	-0.10	-0.15	-0.24
Subjective Risk Judgment	0.04 ^a	-0.23	-0.23
Hunter (1 = yes, 0 = no)	-0.17	-0.16	-0.13
Livestock (1 = yes, 0 = no)	0.10	-0.21	-0.21
Children at Home (1 = yes, 0 = no)	-0.07 ^a	-0.04 ^a	-0.08
Age (yr.)	0.02 ^a	-0.17	-0.02 ^a
Gender (1 = male, 0 = female)	-0.14	-0.07 ^a	-0.05 ^a
Years in Montana	0.02 ^a	-0.27	-0.07 ^a
Education	0.03	0.17	0.08

^a $p > 0.05$

Perceptions of Current Mountain Lion Population Trends

Nearly all respondents (97.8%) knew mountain lions existed in Montana, and 42.8% statewide believed that populations increased 1991 - 1996 (Figure 5.4). The greatest proportion of respondents (44.4%), however, indicated they

didn't know what the population trend had been over the previous 5 years.

Fewer than 3% believed the lion population had decreased.

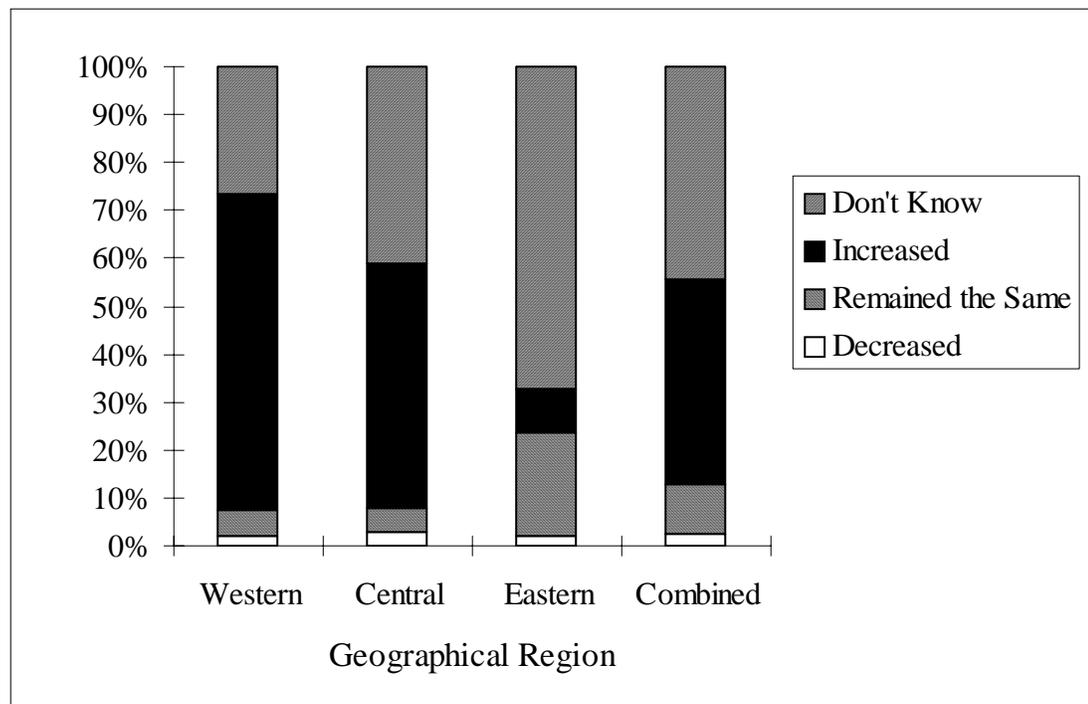


Figure 5.4. The proportion of respondents from western, central, and eastern Montana that believed the mountain lion population in their areas either decreased, did not change, or increased during 1991-1996.

The proportion of Montanans who believed the mountain lion population in their area had increased was greatest in western Montana and least in the east. The eastern strata had the greatest percentage of people who didn't have an opinion about mountain lion population trends or believed they had not changed. In eastern Montana, 65.8% indicated a stable population. Based on nonrespondent telephone interviews, most people perceived that mountain lions are either rare or nonexistent in that portion of the state. The lowest proportion of people who did not have an opinion about lion populations were in the west. The proportion of respondents who believed that the mountain lion population

was higher increased with levels of involvement (Figure 5.5). The level of “don’t know” responses decreased with increased involvement.

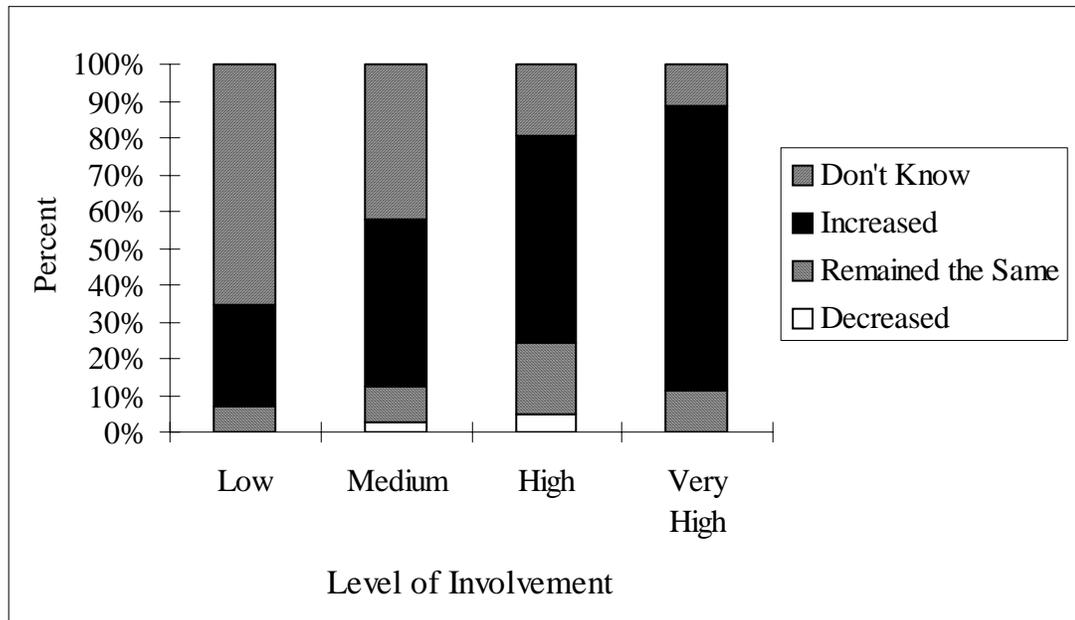


Figure 5.5. The proportion of respondents with various levels of involvement with mountain lions in Montana that indicated a decreased, remained the same, or increased mountain lion population in their areas during the years 1991-1996.

Attitudes Towards Mountain Lions

Two-thirds (67.5%) of Montanans enjoyed the presence of mountain lions, but half (51.8%) indicated they worried about them (Figure 5.6). Respondents who indicated they enjoyed mountain lions without worrying about potential problems lions might cause represented 28.1% of the total. Fewer (17.9%) reported they did not enjoy having mountain lions in areas where they live, work, or recreate. Only 14.6% indicated they had no particular feelings towards mountain lions. More people in western Montana indicated they worried about mountain lions than respondents from the rest of Montana.

A higher proportion of people in eastern Montana expressed no feelings towards mountain lions than the other 2 strata.

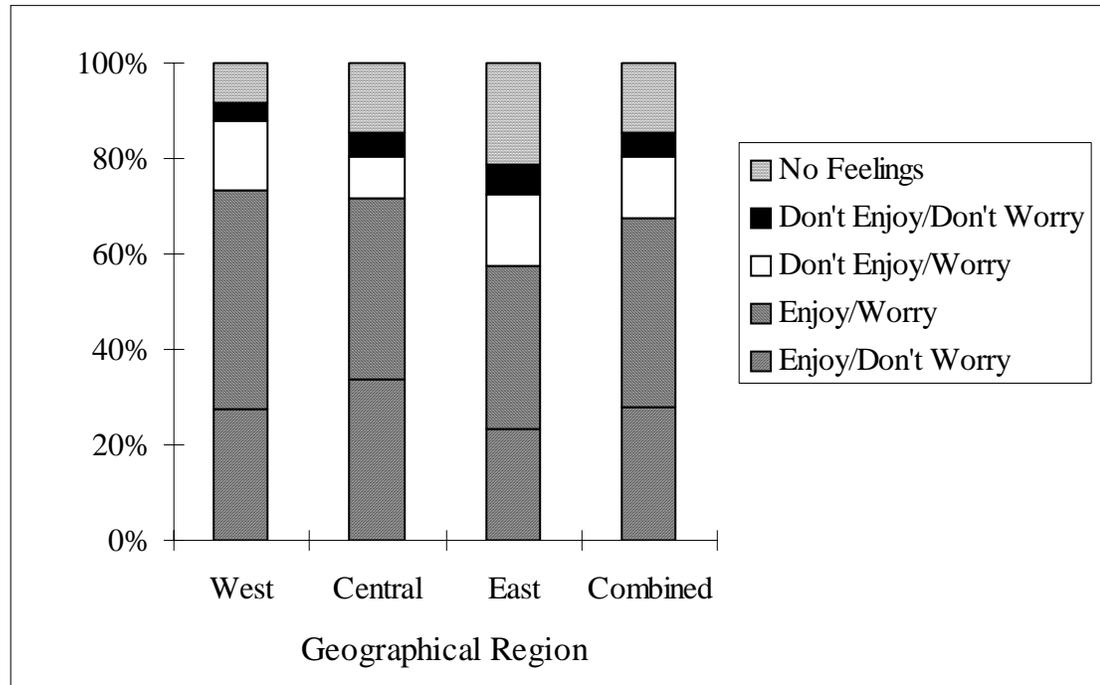


Figure 5.6. The proportion of respondents from western, central, and eastern Montana that expressed different feelings towards mountain lions.

Attitudes towards mountain lions were generally favorable. Based upon a progressive scale from 1 to 5, where 1 was a very negative attitude and 5 was a very positive attitude, the mean ATTITUDE score was 3.26 (SE = 0.035). No significant difference in mean ATTITUDE scores was detected between the 3 strata. Respondents strongly believed the presence of mountain lions is a sign of a healthy environment, and nearly 75% believed lions help maintain deer populations in balance with their habitats (Table 5.4). The presence of mountain lions in Montana enhanced their overall quality of life for nearly 40% of respondents. However, nearly half revealed their underlying concern about living with mountain lions by disagreeing with the premise that the presence of

mountain lions near human habitation increased their quality of life. Responses were divided on whether mountain lions should have the right to exist wherever they may occur, whether mountain lions compete with deer hunters for deer, or whether mountain lions are an unacceptable threat to livestock

Risk Beliefs About Mountain Lions

The majority of Montanans did not consider encounters between humans and mountain lions as something new, but respondents did perceive encounters were increasing in frequency (Table 5.5). A much higher proportion of people in western (66.6%) and central (55.9%) Montana believed risks were increasing than in the east (7.2%). Respondents generally did not believe they were personally at risk from mountain lions. Most respondents indicated they could learn to live with the risks, and that risks were accepted voluntarily. Respondents believed risks from mountain lions were generally understood by experts. A slight inequality between those who benefit from the presence of mountain lions and the people who are exposed to potential risks was thought to exist. Respondents in western Montana had greater mean values for RBELIEF (more risk response) than respondents in eastern Montana ($p = 0.017$). Mean values for RBELIEF did not differ significantly between the west and central nor the central and eastern strata.

Table 5.4. Response of Montanans to belief statements used in the scale to form the variable ATTITUDE regarding mountain lions in Montana.

Belief statements ^a	% response					<i>Factor analysis score</i>
	Disagree	Neither	Agree	\bar{X}	<i>SE</i>	
The presence of mountain lions is a sign of a healthy environment.	14.2	16.7	69.1	3.79	0.04	0.78
The presence of mountain lions in Montana increases my overall quality of life.	29.5	30.6	39.9	3.13	0.05	0.85
The presence of mountain lions near my home increases my overall quality of life.	49.9	28.4	21.7	2.53	0.05	0.84
Mountain lions should have the right to exist wherever they may occur.	44.8	11.0	44.2	3.03	0.06	0.66
Mountain lions help maintain deer populations in balance with their environment.	13.0	12.7	74.3	3.88	0.04	0.74
Mountain lions do not compete with hunters for deer.	39.9	14.0	46.1	3.09	0.06	0.64
Mountain lions are an unacceptable threat to livestock.	45.9	22.5	31.5	3.19	0.05	0.60

^a Scores were derived from a 5-point progressive scale, with 1 indicating strong disagreement, 5 strong agreement, and 3 neither agreement nor disagreement with the statement.

Table 5.5. Response of Montanan's to semantic differential items^a related to risks from mountain lions to human safety in Montana, 1997.

Semantic Differential Item (RTRENDS)	<i>Scale^b</i>					Semantic Differential Item	\bar{X}	SE	Factor analysis score
	1	2	3	4	5				
Encounters between mountain lions and people are something... New	2.9	9.8	17.4	23.0	46.8	Old	4.01	0.04	0.69
The frequency of mountain lion-human encounters are... Increasing	36.2	33.7	17.9	6.4	5.7	Decreasing	2.11	0.05	0.77
(RBELIEFS)									
You are personally at... Great risk	4.6	7.5	15.6	17.5	54.9	No risk	4.11	0.04	0.62
You are... Unable to live with the risks associated with mountain lions?	8.8	12.6	21.0	21.8	35.8	Able	3.63	0.05	0.82
The risks from mountain lions accepted... Involuntarily	8.4	12.3	19.4	23.8	36.0	Voluntarily	3.67	0.05	0.81
The risks from mountain lions... Are Not well understood by experts?	14.5	14.2	21.9	24.1	25.4	Are	3.32	0.06	0.51
Are the people who benefit from mountain lions the same who are exposed to the potential risks? Risks and benefits mismatched	22.9	17.0	25.1	16.0	19.0	Matched	2.91	0.06	0.69

^a Respondents indicated the number between 2 words that best represented their opinion.

^b Values given are percent response for each step along the progressive 1 - 5 scale.

Subjective Risk Perceptions

The most commonly identified level of perceived risk to human safety from mountain lions was approximately 1:10⁶ (Figure 5.7), lowest level of risk above no risk. Only 5.7% of respondents indicated no risk was posed by mountain lions. However, over 55% believed the risks from mountain lions were greater than flying on a commercial airline. Approximately 27% believed the risks were greater than those associated with the operation of farm tractors, and nearly 20% believed the risks were greater than those incurred by riding in an automobile. No difference was detected between strata for the mean level of perceived risk.

A higher proportion of people who desired a smaller lion population perceived risks > 100:10⁶ than those respondents who desired a larger population (Figure 5.8). Those who desired no change in the mountain lion population were intermediate in their perceptions of risk.

Subjective risk judgments were affected by the type of involvement a person had with mountain lions (Figure 5.9). A higher proportion of people in the low INVOLVE category perceived less risk associated with lions than those in the high or very high categories. The differences were expressed at the extremes of the distributions of risk judgments. Whereas respondents with low or medium involvement had a higher proportion of responses in the perceived risk levels < 100:10⁶, those respondents in the high and very high categories of involvement had a lower proportion in the no risk level and a higher proportion in the levels of perceived risks > 100:10⁶. Demographic variables such as presence/absence of children, gender, age, or livestock ownership did not have a discernible influence on risk perception.

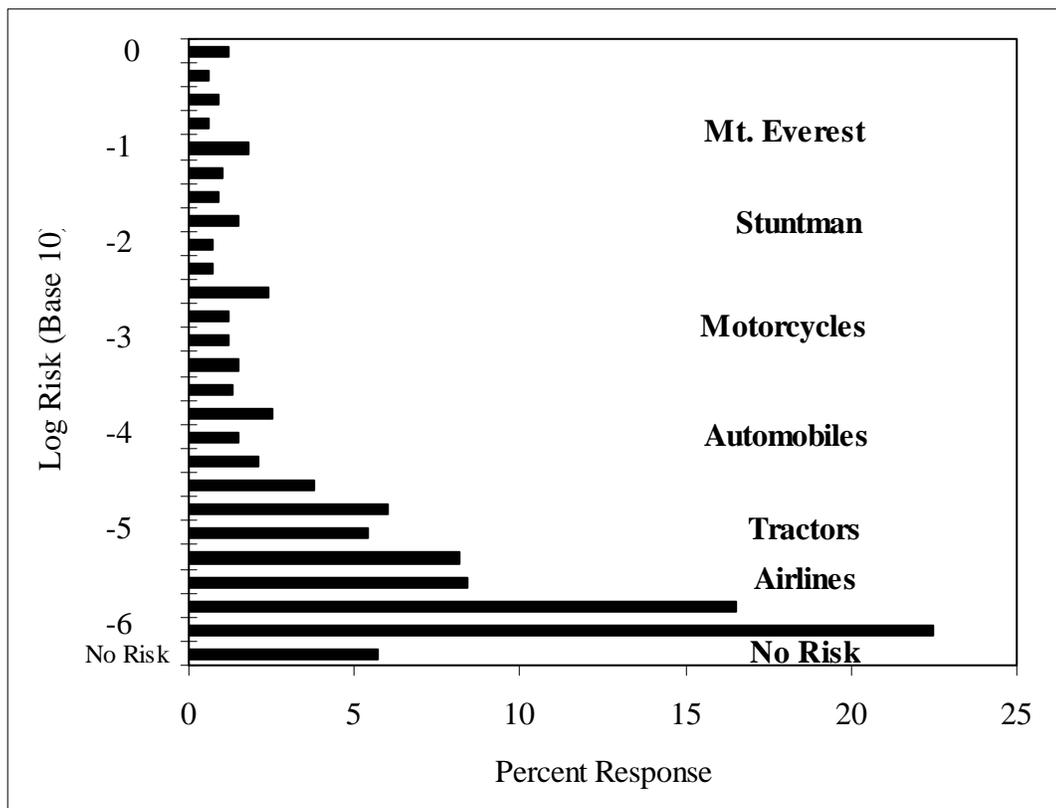
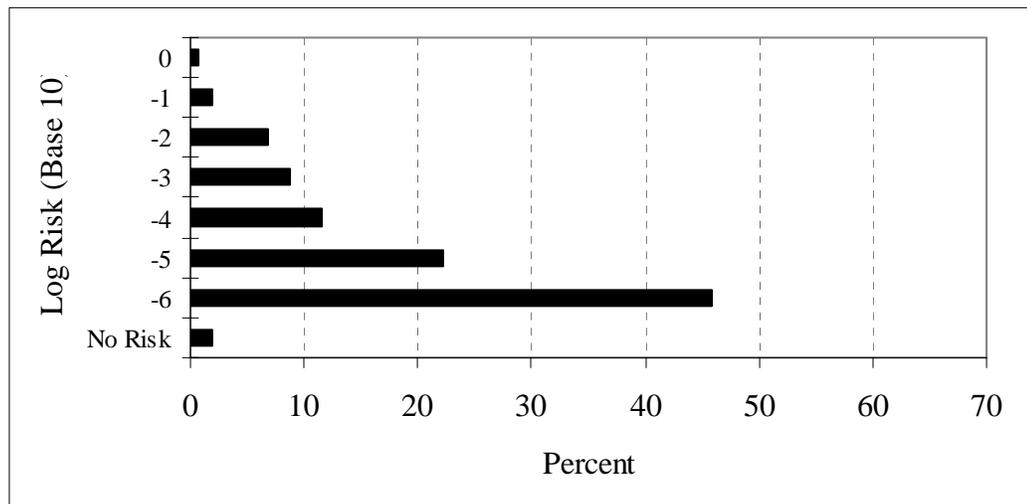
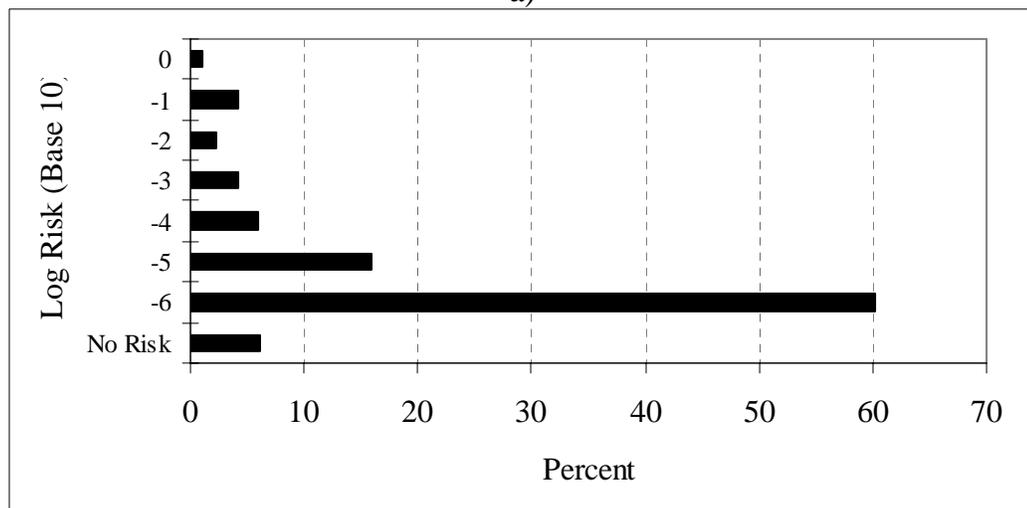


Figure 5.7. The distribution of perceived societal risk to human safety from mountain lions relative to more common risks.



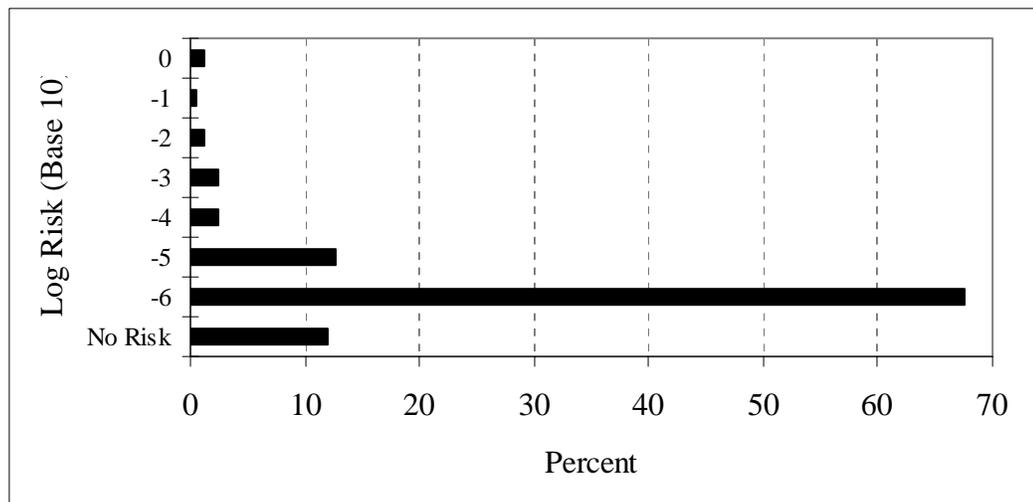
a)



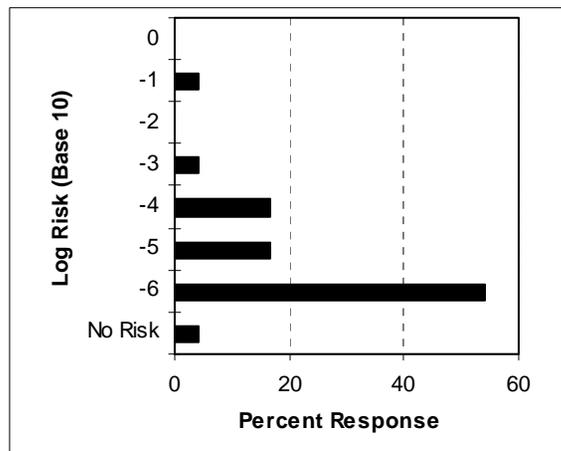
b)

Figure 5.8. A comparison of subjective risk judgments of respondents that desire a) decreased, b) remain the same, and c) increased mountain lion population.

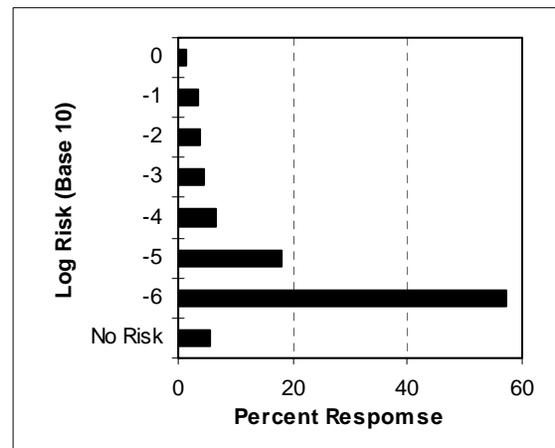
Figure 5.8. (Continued)



c)



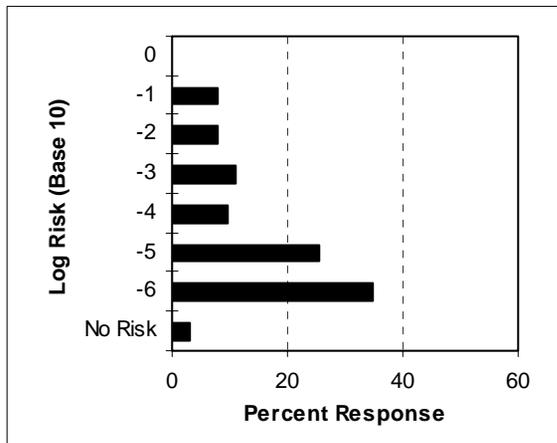
A)



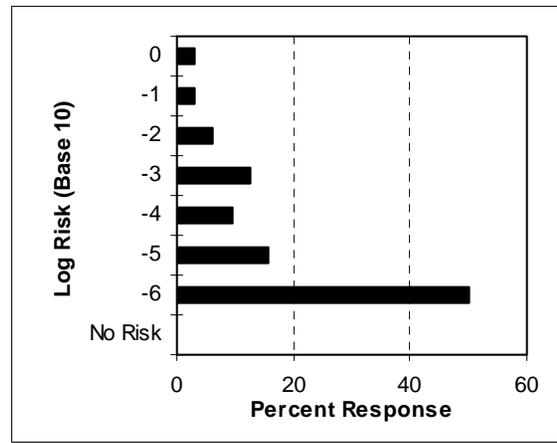
B)

Figure 5.9. A comparison of perceived risks to human health and safety from mountain lions in Montana by level of involvement with mountain lions. A) low, B) medium, C) high, and D) very high.

Figure 5.9. (Continued)



C)



D)

DISCUSSION

Acceptance capacity for mountain lions was influenced most by perceptions of current lion populations, attitudes towards lions, and beliefs about the risks lions present to humans. Perceptions of current mountain lion populations were primarily related to stakeholder involvement with lions and subjective risk judgments. These findings are similar to those reported in a study of stakeholder perception of risks from deer-vehicle collisions (Stout et al. 1993).

The relatively large proportion of people who did not have a preference for future mountain lion populations may indicate a general lack of concern about lions in the everyday lives of Montanans. The similarly high proportion of "don't know" responses may also indicate a certain level of trust in the management agency to make the right decisions regarding mountain lion populations. However, the level of importance placed upon future lion population trends matching people's preferences indicates the seriousness with which stakeholders that have a preference view the lion issue or may indicate stakeholder attitudes about how responsive the wildlife agency should be to their preferences.

Attitudes towards mountain lions and risk beliefs associated with this large carnivore are probably a manifestation of knowledge accumulated over a number of years from varied sources. The most recent information received about an attitude subject generally is the most important in affecting attitudes towards the subject (Eagly and Chaiken 1993). Subjective risk judgments about the potential threat to humans that are a component of those attitudes are probably based on perceptual cues received by the stakeholder; perceptual cues have been identified as a key factor in people's estimate of health risks

(McClelland et al. 1990). People in western Montana, where the highest densities of mountain lions exist (Chapter 3, this ms), are more likely to read or hear about negative lion encounters than people in the eastern portion of that state. Based upon the relevance that media played (vicarious experience) in attitudes towards mountain lions, the media may serve as the primary source for perceptual cues.

Due to the relatively low densities in which mountain lions occur, their secretive behavior, and ruggedness of habitats they occupy, few people have first-hand experience with lions. Most of the people I surveyed who stated they had involvement with mountain lions were referring to vicarious experiences, such as accounts in newspapers, television, and video, or stories they heard second-hand.

The effect of involvement in attitude change is partially related to values held by the individual stakeholder (Eagly and Chaiken 1993). People with high involvement are less persuaded by weak educational messages or arguments than the rest of the public. To achieve a more positive attitude toward mountain lions, different messages will have to address those stakeholders who have had negative, first-hand experiences. Generic conservation messages are not likely to persuade those stakeholders who, based on a negative experience, may feel they have the most at stake or may become the most vocal opposition to conservation of mountain lions.

Geography matters. Residents of cities or towns may believe they have less at stake with mountain lions, and are less likely to perceive risks from lions and may have a lower probability of knowing people who have had first-hand encounters with lions. Despite the presence of mountain lions in eastern Montana (Chapter 3, this ms), people there do not view mountain lions as a

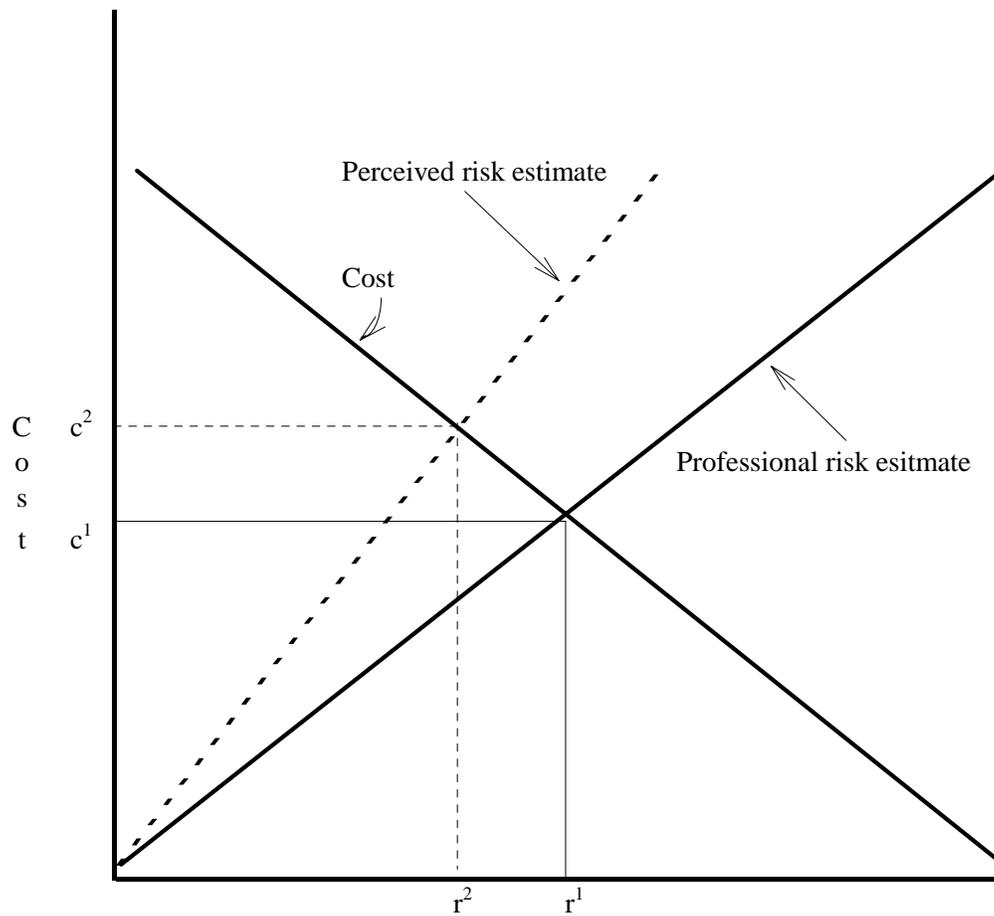
salient issue. The media in eastern Montana may not view the mountain lion as an issue yet, and hence the public has less exposure to stories about mountain lions in that part of the state.

Involvement is also partially dependent upon the types of activities in which people engage. My data suggest most people in western and central Montana participate in outdoor activities that can put them in contact with mountain lions. A smaller proportion of people in eastern Montana participate in any such activities when compared to their counterparts in the western two-thirds of the state. Certain groups of people, most notably big game hunters and livestock producers, are more likely to perceive competition with mountain lions. Those stakeholders may feel more is at stake (risk) with lions and actively participate in traditional forms of public involvement.

The difference between perceived risk by stakeholders and the risk perceived by agencies potentially creates a policy dilemma with concomitant costs. Whereas the majority of stakeholders in Montana perceive relatively little risk from mountain lions, a segment views the risks higher than any realistic estimate.

Figure 5.10 displays a hypothetical, but a plausible cost:benefit depiction of perceived risks from mountain lions in Montana. For every level of risk (r), which is partially a function of lion population density, there is an associated cost (c) of mountain lion management. Costs could be measured in mountain lions killed, or in lost opportunities to have more lions in an ecosystem. The costs also may be born by management in time required for conservation officers to investigate damage complaints or in other animal damage control actions. Information and education programs designed to support larger

populations of mountain lions also require higher costs than those at lower lion population levels.



Risk as a function of mountain lion density

Figure 5.10. A cost:benefit display of the costs associated with different estimates of perceived risk to humans from mountain lions.

Line A depicts the risk function as estimated by experts, and the perceived risk function is depicted by line B. Costs associated with each level of risk are estimated by line C. The intersection of line A with C has a cost (c_1) related to a r_1 level of risk. Perceived risk intersects C at risk level (r_2) and cost (c_2). The elevated perceived risk has a net increase in cost depicted by $c_2 - c_1$.

Wild swings in perceived risk due to a recent attack reported in the media can be predicted to have even greater short term costs.

Risk is only one of many attributes that people must use in decisions about acceptance of a new technology (Ottway 1992) or wildlife populations (Decker and Purdy 1988). Bright and Manfredo (1996) indicated that emotion was a primary factor that influenced people's intention to support wolf reintroduction in Colorado. The decision to be for or against reintroduction of a large carnivore involves a type of risk assessment. Risk evaluation is tied closely to values, beliefs, and attitudes. A person cannot define risk and make a choice without involving values (Slovic 1987). My data indicate mountain lions are valued in Montana. People appreciate the role of mountain lions in an ecosystem as expressed by the belief that lions are a sign of a healthy environment, and that lions help maintain deer populations in balance with their habitat. Some people perceive benefits from mountain lions as indicated in the common belief that lions increase the overall quality of life in Montana, and by the notable percentage of people who indicated they enjoy mountain lions living in areas they live, work or recreate. However, a "Not in my backyard" attitude was detected when the same question about quality of life was asked with regard to lions near the homes of respondents. These findings suggest people appreciate and tolerate lions in wildland settings, but are not especially tolerant of lions in habitats occupied by humans.

MANAGEMENT IMPLICATIONS

Several important management implications surface from my findings. First, a base of conservation-oriented values exists on which to build more positive attitudes toward carnivores and lions in particular. Second, intolerance of mountain lions in close proximity to human habitation suggests that housing development represents a long-term loss of habitat both in traditional terms of a physical loss and also from lower acceptance capacity of mountain lions. Last, wildlife managers can potentially affect the acceptance capacity for mountain lions by addressing variables that affect attitudes, risk perception, and perception of current population trends as identified in my model.

Montanans have a relatively positive attitude toward the species despite concerns for problems mountain lions may cause. Appreciation exists for the role mountain lions play in the environment. This provides a basis of support that can be built upon for sharing a human-dominated environment with a potentially dangerous animal. Big game hunters and ranchers that view the mountain lion as a competitor, and those people with first-hand negative encounters, should be the focus of conservation-oriented communication efforts that are stronger than the general messages provided to the broader group of stakeholders.

A general intolerance for mountain lions near human habitation reinforces the long-term consequences of land uses such as subdivisions. Human habitation is not only a loss of physical habitat, but also a serious alteration of the social landscape. The intolerance of mountain lions near homes means that rapid urban sprawl and isolated subdivision development in the West (Riebsame 1996) may deplete the overall acceptance capacity for the species.

Wildlife management might benefit from thinking about the concept of risk in the context of mountain lion management (Knuth et al. 1992). Risks can be thought of as having 4 components or processes that are relevant to wildlife management (Merkhofer 1987): a hazard (e.g., mountain lion populations and behavior); an exposure process or a process that permits a hazard to affect the stakeholder (e.g., jogging in the mountains or foothills); an effects process or the consequences to the stakeholder (e.g., lion depredation or perception of being threatened); and a valuation process or individual and social value judgments towards the hazard and the other processes (consequent utility).

Wildlife management has traditionally focused on modification of wildlife populations to alter risks. Translocation is often used to separate a potentially dangerous animal from situations that may result in heightened concern among stakeholders (Riley et al. 1994). Direct manipulation of mountain lion populations (Chapter 4, this ms.) or their habitats (Chapter 3, this ms.) are more broadly applied approaches designed to affect biological carrying capacity or an organism's ability to realize that capacity. Management that involves removal or destruction of animals who pose a threat to humans may be needed to maintain a level of acceptable risk among Montana stakeholders. If the level of perceived risks increases because of no action on the part of management, preferences for smaller lion populations may occur. A tolerance limit, based upon attitudes, probably exists and if exceeded may be difficult to regain.

Attempts have been made recently to alter the exposure and effects processes through modification of human behavior such as grazing practices designed to minimize depredation (Jackson and Nowell 1996). Targeted control of specific problem animals is also a method commonly used to

manipulate the effects process. Restrictive regulations on land development are one alternative, but the jurisdictional complexities and political sensitivity have limited the effectiveness of this management method (Keiter and Locke 1996).

An alternative or supplementary approach is to direct management efforts toward modification of wildlife acceptance capacity through application of risk communication. Keeney (1995) provides guidelines for structured thinking about risk communication that may be helpful to wildlife managers concerned with large carnivores. First, the issues raised by a risk problem need to be acknowledged. The complexities of the problems should be explicitly displayed so that everyone understands the potential management alternatives that can be developed. Communication targeted towards increasing favorable attitudes and knowledge of stakeholders will increase acceptance capacity (Knuth et al. 1992). People in urban areas need to be aware of the concerns of the rural-ranch community. Similarly, members of the rural-ranch community must be made aware of the values held by other people in Montana. Many people in rural areas, presumably those exposed to the higher everyday risks from mountain lions, have learned to live with those risks. Facilitation of communication between groups' different stakes in an issue can be a potentially powerful management technique (Gregory and Keeney 1994).

Objectives for each risk problem need to be clarified. No level of management can make life risk free (Keeney 1995). The reasons to take action should be clearly and explicitly stated. Personal decisions can reduce health risks far greater than any government actions (Zeckhauser and Viscusi 1990). Information and education programs should focus on empowering individuals with knowledge that encourages each person to affect their own behavior. Informative guidelines on how to make livestock less vulnerable to mountain

lions (Jackson and Nowell 1996) and how to make subdivisions and areas around homes less attractive to the big cats should be infused into localized management schemes. Dissemination of information on what to do in case of an attack will also provide people with knowledge to affect their sense of security. However, care must be exercised to ensure communication of this information does not become another source of perceptual cues that increases perceptions of risk.

The role of judgments about facts and values related to each risk problem must be identified. Differences of opinion about what actions are appropriate to address risk problems generally stem from different factual judgments or different value judgments. Experts (e.g., biologist, university researchers) should provide an estimate of the risk levels so that people can have a basis for decisions. However, perspectives of different stakeholders should be considered. Questionnaires, like the one described in this paper, are 1 potential forum for collecting information about stakeholder values and perceptions. Another reasonable and useful way is to include stakeholders in risk assessment and management (Gregory and Keeney 1994, Decker and Chase 1998).

Facts about risks should be communicated consistently. People pay attention to the media, and they want to be informed. Fiorino (1989) succinctly stated “The lay public are not fools.” It is vital that the experts communicate consistent facts to interest groups. Discrepancies in risk assessments and public perceptions can lead to a general breakdown of trust in the scientific, governmental, and industrial managers (Slovic 1992). Experts often dismiss risk altogether or dismiss stakeholder perceptions of risk (Ottway 1992). If stakeholders who perceive risks from mountain lions read in a newspaper that

an expert (e.g., wildlife manager or university researcher) rejects or trivializes the notion of risks from lions, there is potential for erosion of public perception of an agency's or profession's credibility.

CHAPTER SIX

INTEGRATION OF ENVIRONMENTAL, BIOLOGICAL, AND HUMAN DIMENSIONS FOR MANAGEMENT OF MOUNTAIN LIONS (*PUMA CONCOLOR*).

INTRODUCTION

Wildlife management strives to become more comprehensive by applying a multi-disciplinary approach to issues facing managers today (Decker et al. 1992). Meffe and Veiderman (1995) identified 6 strategies they felt must be adopted if wildlife managers are to maintain an effective role in the development of resource policy. Their suggestions included an multidisciplinary approach to working on issue-oriented problems while maintaining broad temporal and spatial perspectives. Expanding populations of mountain lions (*Puma concolor*) in western North America provide a lucid example of the need for a more comprehensive approaches to wildlife management. Considered rare as late as 1960, mountain lions have become a perceived threat to human safety in many areas of western North America.

Historically, mountain lion management primarily focused on their eradication as a threat to humans and livestock (Nowak 1976). Compared to other large fauna, little scientific research had been conducted on the mountain lion because of its status as a perceived nuisance predator. The pioneer research of Hornocker et al. (1970) and Seidensticker et al. (1973) in the same Idaho study area provided most of the scientific basis for management before 1980 (Russell 1978, Anderson 1983). Mountain lions were viewed as secretive animals that occurred in low abundance through a self-regulating system of land tenure. Through the late 1980s and 1990s mountain lion populations flourished throughout the West (Padley 1997) . Wildlife managers were

unprepared for the increased frequency of attacks by mountain lions on humans and their pets, along with numerous other lion-human incidents in some of the West's largest cities as well as rural communities (Braun 1992). A comprehensive understanding of the factors that affect population growth in mountain lions and the factors that affect stakeholder preferences for mountain lion populations is needed to enhance management.

My approach to an integrative understanding of the mountain lion issue was to decrease the complexities of mountain lion management into three dimensions: the environmental, the biological, and the human. The environmental dimension includes all aspects of the environment such as food, water, cover, and space that normally affect biological carrying capacity (BCC) of an organism (Macnab 1985). The biological dimension includes the endogenous processes that result from an organism's response to the environment, and encompasses such processes as birth, death, behavior, and subsequent population dynamics. The human dimension includes all human-oriented aspects of the resource management ecosystem (Decker and Chase 1998). This includes social-psychological characteristics such as what people think and do regarding wildlife (Decker and Libscomb 1991), and institutional arrangements to manage the people and resources (Knuth and Nielsen 1989). An important component of the human dimension is wildlife acceptance capacity (WAC). A concept adapted from biological carrying capacity, WAC is an estimate of the maximum perceived numbers of a particular wildlife species that are acceptable to people in an area (Decker and Purdy 1988).

By viewing the decision/effects space of mountain lion management as a triangle, the relationships and interactions of the environmental, biological, and human dimensions can be discerned (Figure 6.1). For example, in Figure 6.2,

polygon A represents the hypothetical decision/effects space encompassed by a land use issue such as subdivision development. There is a clear alteration of the environmental and human dimensions, but only a subtle effect on the biological over the short-term. In the case of mountain lions, the effect on the biological dimension depends on geographical proximity of the land-use changes to occupied lion habitat.

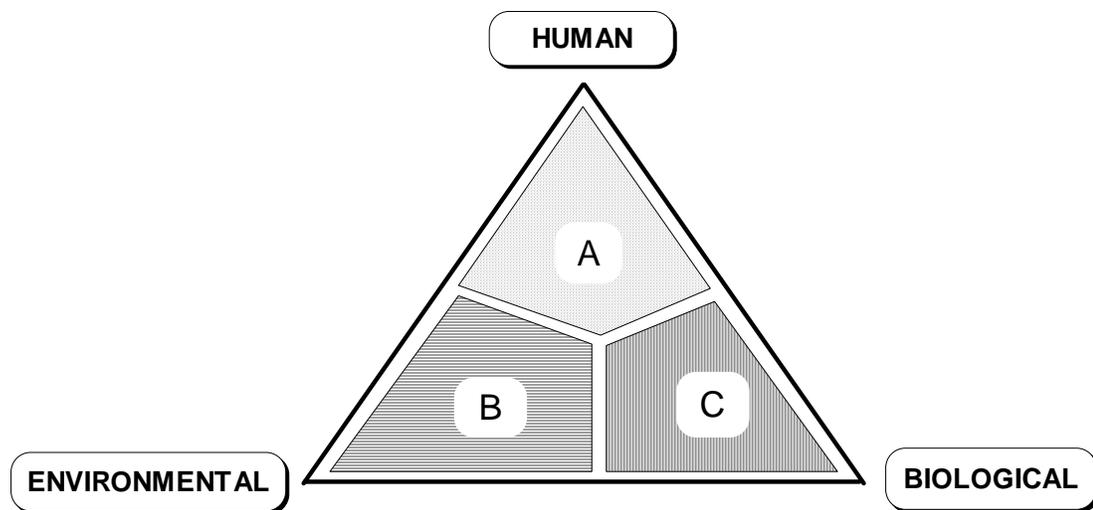


Figure 6.1. The spectrum of implicit decision/effects of the human, environmental, and biological dimensions associated with wildlife management.

Polygon B represents the decision/effects space of a change in a mountain lion hunting season. There is some alteration of the human dimension, but proportionally more significant effect occurs to the mountain lion population as it is affected by changes in adult survival.

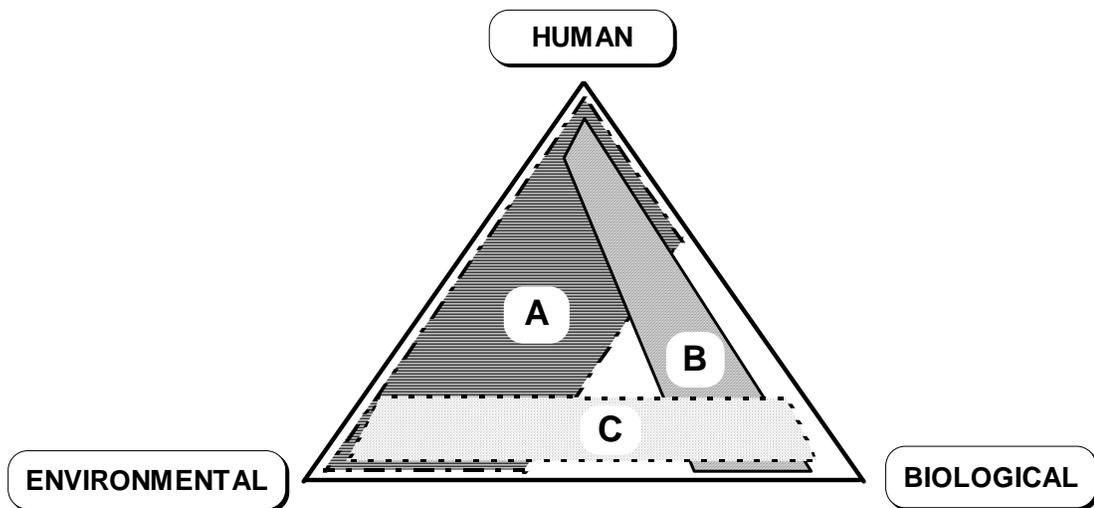


Figure 6.2. The space of implicit decision/effects associated with mountain lion management. (A) subdivision development, (B) hunting regulations, and (C) predator-prey interactions.

Predator-prey interactions are delineated by polygon C. These interactions are a function of habitat and the behavior of mountain lions and their prey (Seidensticker et al. 1973). People are not normally involved in the interactions unless a prey species is one that is also desired by humans such as deer, livestock, or pets. The decision/effects space then swells to include all 3 dimensions. Few situations in carnivore management are more controversial than the allocation of prey between a large carnivore and humans (Estes 1996). Mountain lion attacks on humans (Beier 1992) include all dimensions of management and surpass predator-prey issues in controversy and reaction from stakeholders.

Each management action has its own temporal or spatial context and scale depending on the circumstance (Figure 6.3). Management strategies that focus strictly on mountain lion populations, such as hunting regulations, can

occur quickly, be focused on individual population units, and have nearly immediate effects on population growth of mountain lions (Chapter 4, this ms.).

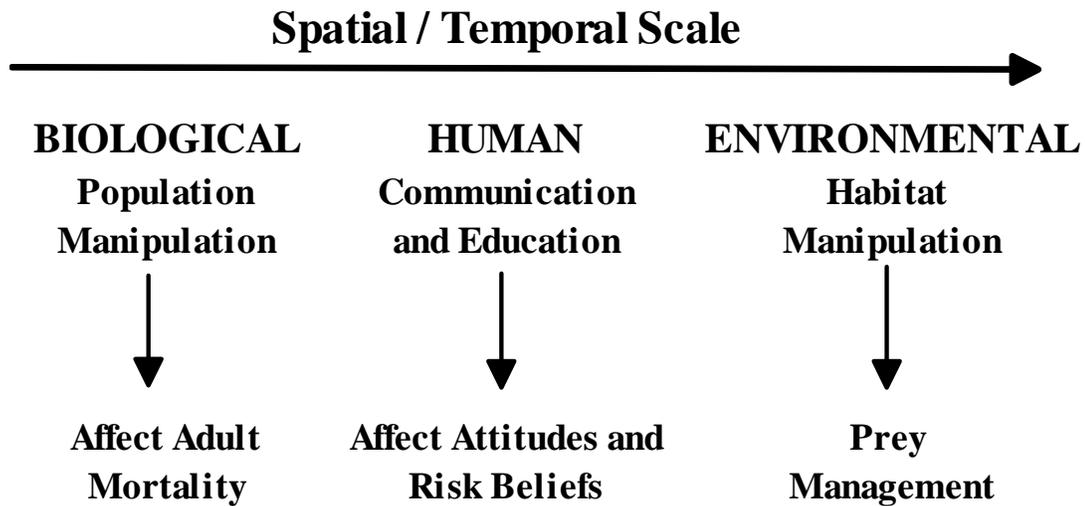


Figure 6.3. Spatial and temporal scales associated with different dimensions of mountain lion management (Adapted from Litvaitis et al. 1996).

Modification of WAC through communication, education, and stakeholder participation requires time (Decker and Purdy 1988) and generally occurs on a broader scale than individual lion population units. Perceptions of current lion population trends, attitudes towards lions, and beliefs about risks to humans from mountain lions are key determinants in stakeholder WAC for future mountain lion populations (Chapter 5, this ms). Perception of current lion populations is partially a function of communication, both interpersonal and through various forms of media. Formation of attitudes towards mountain lions is in turn a function of past involvement with lions and perceptions of risks to human health and safety. Education and communication programs designed to affect WAC for mountain lions should focus on altering human

behavior to minimize direct contact between mountain lions and people. Communication should also focus on modifying perceptions of risk to human health and safety from mountain lions.

Management that attempts to modify the environmental dimension for mountain lions occurs at broadest scale and over the longest time frames. Modification of the environmental dimension is synonymous with management of biological carrying capacity. There are management actions, such as an individual timber sale, that may alter the environment, but most are too small to affect significant change in populations of large, roaming carnivores such as mountain lions (Litvaitis et al. 1996). Land-use takes time to manifest itself in mountain lion population changes, and ungulate distribution and abundance are normally intermediate processes in the chain of effects (Chapter 3, this ms.).

Management matrices (Knuth and Nielsen 1989) provide a helpful way of identifying multidisciplinary approaches for management of mountain lions. Figure 6.4 displays management options under a common management challenge of trying to match direction of population management of mountain lions with their population status. I have portrayed 3 qualitative population levels as high, medium, and low. Ideally, a continuous scale of population levels could be envisioned. However, where accurate quantitative estimates of population levels are lacking, as in the case of mountain lions, these 3 categories may be sufficient. In terms of objectives, there are 3 directions that management can theoretically influence populations. Populations can be increased, decreased, or held stable. Within each intersection between management direction and population status, wildlife management has options to affect 1 or more of the 3 dimensions of management.

A review of options under 2 different population levels and management directives provides useful examples of an integrated approach to mountain lion management. The situation in the upper right corner of the matrix in Figure 6.4 depicts a situation where the population status is believed high and the management direction is for a decreased population. This scenario existed in western Montana during 1997.

To effect a decrease in mountain lion abundance, management could attempt to modify the environmental dimension through reduction of cover or ungulate abundance. As discussed earlier, management targeted toward the environmental dimension generally requires an extended time frame to realize changes in lion numbers through modification of the biological carrying capacity. There likely will be a lag between reduction of prey and a response in BCC. In addition, time is required to implement changes in hunting seasons or other mechanisms that affect ungulate abundance.

A more rapid approach to lowering lion populations is to influence adult female survival (Chapter 4, this ms.). Hunting or animal damage control actions that decrease annual adult female survival below 68 % will have an immediate negative effect on population growth rates. Adult male mountain lions are an important internal population regulator that affect survival of all age classes and limit the number of potential territories on a landscape through their territorial behavior (Logan et al. 1996). Another possible management strategy to lower the number of lions in an area could be to lower mortality of adult males, allowing them to play a role in regulating populations.

Lion Population Status	Management Dimension	Population Management Direction		
		Increase	Stable	Decrease
High	Env.			
	Biol.			A
	Human			
Medium	Env.			
	Biol.			
	Human			
Low	Env.			
	Biol.	B		
	Human			

Figure 6.4. An integrated mountain lion management matrix that depicts potential management situations under various population levels and population management directives.

If the goal is to decrease populations, communication strategies should be used to increase public awareness of the reasons for this management direction.

Communication should focus on urban audiences that are least sympathetic to hunting of mountain lions in Montana (Riley, unpublished data). Based upon a model of the variables that most affect WAC of mountain lions in Montana, lion population trends and potential risks from lions should be communicated (Chapter 5, this ms.).

If mountain lion populations are low and the directive is to increase populations, as depicted by matrix B in Figure 6.4, there are a number of management actions that can be taken to facilitate population growth. Increased ungulate abundance would provide an environmental base on which lion density should increase (Chapter 3, this ms). Increases in the distribution of prey species also should help increase the distribution of mountain lions.

Protection of mountain lions from human-induced mortality should promote growth in the lion population assuming the environmental needs have been addressed. Partial reduction in adult males may facilitate population growth through reduced intraspecific mortality and the inability of subadult males to maintain large territories (Logan et al. 1996).

Human dimension approaches should focus on enhancing attitudes towards mountain lions, communicating low lion population levels that exists, and maintaining a low level of perceived risk to humans. All stakeholders should be informed of human behaviors that reduce risks from mountain lions such as not jogging in mountain foothills, landscaping to discourage deer from coexisting with people, and livestock management practices that minimize conflicts with lions. Decreased direct involvement with mountain lions increases the probability that people will be more tolerant of lions (Chapter 5,

this ms.). As in the first example, education early in the process that modifies human behavior and subsequently minimizes direct involvement with mountain lions, should help promote positive attitudes towards lions. However, overemphasis on the potential dangers posed by mountain lions may heighten risk perception and subsequently lower WAC (Chapter 5, this ms.). Use of risk communication techniques that lower perceived risks from lions will also facilitate more positive attitudes towards lions (Chapter 5, this ms.).

Communication of benefits of mountain lions in ecosystems and the role of lions in maintenance of a perceived balance between ungulates and their habitats should also create more positive attitudes towards mountain lions.

Addressing more than 1 management dimension at a time makes mountain lion management more comprehensive and should improve the probability of successfully achieving goals. Management focused only on a single dimension will likely achieve short-term success. The dynamics of the other dimensions are expected to surface as new management dilemmas. Because all management in some way affects or is affected by the human dimension, a single focus approach may result in unexpected concerns by stakeholders that impede implementation of management activities (Curtis and Hauber 1997). In these situations, having alternative management options in other dimensions may help achieve desired goals.

Management that affects the environmental or biological dimensions has its own set of stakeholders that may be separate from mountain lion issues under consideration. For instance, any attempt to affect cover will have to address concerns of people who have a stake in land management. Those stakes may be wildlife-oriented, commercial, or based in esthetics of landscapes and viewsheds. In many cases, there is need to modify ungulate populations.

Any management directed toward ungulate distribution or abundance must also address concerns of traditional stakeholders such as deer hunters and non-traditional groups such as homeowners (Curtis and Hauber 1997).

Conclusions

The primary goal of integrative analysis is to increase understanding and enlighten decisions, not necessarily to provide solutions in the sense of final or absolute answers (Goodwin and Wright 1991). An integrative approach is a problem solving process that emphasizes inclusion of all potentially affected dimensions of management (Decker and Chase 1998). By definition, there are no single dimension solutions.

Solutions must be derived on a case by case basis and adapted to specific local situations. Slobodkin and Dykhuizen (1991) stated, "Science is concerned with creating an intellectual model of the material world. Technology is concerned with procedures and tools and their general use to gain or use knowledge. Practice is concerned with how to treat individual cases. Confusing the three can be dangerous." Wildlife management operates by applying principles to individual cases (Caughley and Sinclair 1994). The models and frameworks I have presented are intended to help guide thinking about mountain lion management and provide a greater array of options and alternatives in the pursuit of solutions.

Considerable overlap exists between the environmental, biological, and human dimension, and many interrelationships between dimensions are subtle. The management options brought to bear on any particular issue depend on the interplay between the different dimensions. What happens in one dimension generally affects another. Because natural sciences are inherently value-laden

(Shrader-Frechette and McCoy 1993), wildlife science can not propose unequivocal single solutions. Whereas there are processes that may be exclusive to only one dimension, all that involve management are affected by or affect the human dimension.

APPENDIX I

RESEARCH NEEDS FOR MOUNTAIN LIONS IN MONTANA.

One important purpose of an integrated analysis is to identify gaps in knowledge that should be a focus of further research. The following are research topics listed by topical area and in order of priority (within each dimension) set by the author.

Environmental Dimension

This project identified key prey species that promoted population growth in mountain lions. There is a need to better understand the food web relationships between the environment, prey species, and mountain lions. The primary causes for population growth and distribution of ungulate species are necessary if management wishes to affect the biological carrying capacity of mountain lions.

Biological dimension

Techniques to accurately estimate numbers of mountain lions in a variety of landscapes are needed. The ability to quantitatively assess mountain lion populations is critical if management is to set numeric objectives for those populations. Adaptive management of mountain lions will be impossible unless a mechanism for accurately monitoring population response to management alternatives is developed.

Techniques to accurately age mountain lions need refinement so that age-structured population models can aide in monitoring lion populations. The requirement for each mountain lion skull to be turned over to MDFWP provides

a potentially large sample of ages to use in analyses. Current inaccuracy in aging estimates prohibits full use of this potentially useful data.

The 3 ecoregions identified in Montana have apparent differences in biological carrying capacity for mountain lions. This project determined some initial ecoregion-specific estimates of relative mountain lion densities and the key prey species associated with those respective populations. Further research is needed into the mechanisms of mountain lion population growth under each set of general environmental conditions that exist in the different ecoregions. Populations may be more prone to fluctuations in the Intermountain and Prairie Ecoregions where climatic fluctuations are greater than in the Montane Ecoregion. Understanding lion population responses in these situations is vitally important if management programs are to be sensitive to the needs of mountain lions across Montana's diverse landscape.

Human dimension

Of all dimensions of mountain lion management, the human dimension may be least understood. This project presented an initial analysis of factors that affect stakeholder preferences for mountain lions in Montana.

Communication was identified as an important aspect of involvement with mountain lions and subsequently in formation of attitudes that affect WAC for lions. A better understanding is needed of sources and channels of communication that are most important in promoting informed stakeholders.

In the absence of accurate estimates of mountain lion populations, management goals and objectives often may be based upon perceptions of stakeholder or agency personnel WAC for mountain lions. Local stakeholder involvement in setting population objectives may be the most effective

mechanism for assuring all concerns are taken into consideration. Mechanisms for public participation in wildlife management are still evolving (Gynn and Landry 1997, Decker and Chase 1998). Further research is needed to develop techniques that work best for Montana and for the unique attributes of mountain lion management.

This project was one of the first to investigate risk perception as an important component of stakeholder WAC for a large carnivore. Additional research may help identify risk communication techniques that provide managers a mechanism for modifying concerns about animals that present low probability-high consequence risks to humans.

Mountain lion management in Montana

The absence of techniques to accurately assess mountain lion populations will make it nearly impossible to know if and when lion populations have been overexploited. Sensitivity analyses of lion population models suggest that population growth is most sensitive to changes in adult survival rates. Hunting mortality can easily exceed the potential for populations to sustain themselves (Logan et al. 1996). Alternatives to a quota system should be investigated. Spatially structured harvest systems (McCullough 1996) that do not rely on accurate population enumeration may provide a system that simultaneously provides for long-term conservation of mountain lions and a yield for sport harvest. Montana's physiography, land use patterns, and urbanized human populations may provide an optimal environment for such management systems.

APPENDIX II

AN ANALYSIS OF THE NUMBER OF MOUNTAIN LIONS (*PUMA CONCOLOR*) AND WOLVES (*CANIS LUPUS*) KILLED UNDER THE BOUNTY SYSTEM IN MONTANA, 1884 - 1962.

Mountain lions were listed on the first state-wide Montana bounty law passed in 1884. The estimated number of lion hides presented for payment varied from 177 in 1908 to 0 in 1932 (Figure AII.1). Despite demand and an increasing bounty payment, lion hides became scarce in the late 1920's and ceased being presented for payment in 1930. Written bounty records after 1932 have been lost so that comparable data are unavailable. Conflicting reports exist. Nowak (1976) indicated 191 mountain lions were taken between 1930 and 1950 under federal animal damage control. Montana Fish and Game Commission (unpublished files) suggest fewer than 5 annually were taken statewide under the bounty system until 1950. The number taken then increased through the 1950s to 167 in the 1961-1962 biennium (Riley 1992).

Bounty prices increased from \$8.00 (\$269 in 1995 dollars) per lion and \$1.00 (\$34 in 1995 dollars) per wolf in 1884 to \$25.00 (\$270 in 1995 dollars) for either species in 1930. Wolf pup prices increased from 50 cents in 1884 (\$17 in 1995 dollars) to \$5.00 (\$54 in 1995 dollars) in 1930.

Records taken from original bounty record books permit enumeration of bounty take by counties as they existed in 1900 (Table AII.1 and 2). An inverse relationship exists between ecoregions where the highest densities of wolf and lion pelts were presented for bounty (Figure AII.2). The mountain lion take was greatest in the Montane Ecoregion of western Montana and the take of wolves was greatest in the Prairie Ecoregion type. Only Park County, in southwest Montana adjacent to Yellowstone National Park was in the top 5 counties for density of lion and wolf take (number 5).

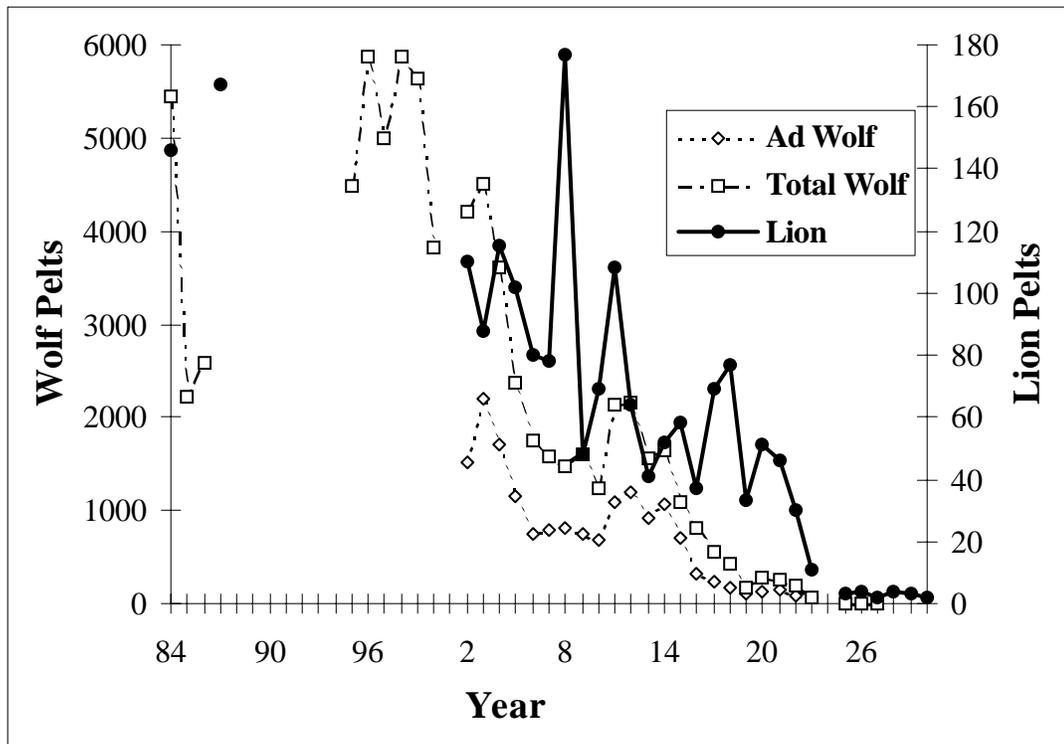


Figure AII.2. Number of mountain lion and wolf hides presented for bounty payment in Montana, 1884 - 1931.

A negative linear relationship ($r^2 = 0.16$, $p < 0.001$) occurred between the density of lion pelts and the density of wolf pelts on a county by county basis (Figure AII.3). The negative relationship is stronger ($r^2 = 0.259$, $p = 0.015$) if Flathead County (Flathead, Lake and Lincoln counties in 1997) is eliminated from the sample. Flathead County was high in both lion and wolf bounty take.

Table AII.1. The total wolf and mountain lion bounty payments by Montana counties, 1900 - 1931.

1930 County Name	Adult Wolf	Wolf Pup	Total Wolf	Mountain Lion
Beaverhead	597	116	713	28
Big_horn	203	446	649	0
Blaine	80	125	205	1
Broadwater	77	6	83	6
Carbon	279	105	384	2
Carter	5	21	26	0
Cascade	694	558	1252	31
Chouteau	1111	2503	3614	35
Custer	2448	3082	5530	4
Daniels	1	0	1	0
Dawson	1083	1167	2250	8
Deerlodge	53	8	61	0
Fallon	51	118	169	0
Fergus	1043	1553	2596	35
Flathead	492	16	508	791
Gallatin	106	147	253	18
Garfield	3	25	28	0
Glacier	12	0	12	1
Golden Valley	3	0	3	0
Granite	31	2	33	20
Hill	76	55	131	0
Jefferson	71	2	73	9
Judith Basin	5	4	9	0
Lake	0	0	0	3
Lewis and Clark	250	119	369	33
Liberty	9	13	22	0
Lincoln	738	14	752	105
McCone	4	17	21	0
Madison	122	18	140	14
Meagher	612	243	855	29
Mineral	0	3	3	8
Missoula	20	8	28	148
Musselshell	157	246	403	0
Park	405	58	463	67
Petroleum	0	0	0	0
Phillips	61	66	127	0

Table AII.1 (Continued)

1930 County Name	Adult Wolf	Wolf Pup	Total Wolf	Mountain Lion
Pondera	1	8	9	0
Powder_river	7	11	18	0
Powell	74	2	76	36
Prairie	29	24	53	0
Ravalli	4	0	4	43
Richland	11	37	48	0
Roosevelt	0	0	0	0
Rosebud	3278	3109	6387	1
Sanders	6	0	6	49
Sheridan	4	10	14	0
Silverbow	56	6	62	9
Stillwater	19	15	34	0
Sweet Grass	342	184	526	16
Teton	237	780	1017	5
Toole	0	5	5	0
Treasure	3	2	5	0
Valley	808	1116	1924	7
Wheatland	1	0	1	0
Wibaux	4	0	4	0
Yellowstone	806	868	1674	0
Total	16592	17041	33633	1562

Table AII.2. The total wolf and mountain lion bounty payments, 1900 - 1931, adjusted for 1900 Montana county boundaries.

County (1900)	Area (Mi ²)	Adult Wolf	Pup Wolf	Total Wolf	Total Lion	Adult Wolf Density	Pup Wolf Density	Total Wolf Density	Total Lion Density
BEAVERHEAD	4579.57	597	116	713	28	0.1303616	0.02533	0.155691	0.006114
BROADWATER	1211.50	77	6	83	6	0.0635575	0.004953	0.06851	0.004953
CARBON	2530.62	279	105	384	2	0.1102495	0.041492	0.151741	0.00079
CASCADE	3425.54	694	558	1252	31	0.202596	0.162894	0.36549	0.00905
CHOTEAU	16244.26	1276	2701	3977	36	0.0785508	0.166274	0.244825	0.002216
CUSTER	23100.56	5995	6789	12784	5	0.2595176	0.293889	0.553407	0.000216
DAWSON	13245.54	1134	1270	2404	8	0.0856137	0.095881	0.181495	0.000604
DEER LODGE	3284.48	127	10	137	36	0.0386667	0.003045	0.041711	0.010961
FERGUS	8993.53	1210	1803	3013	35	0.1345411	0.200477	0.335018	0.003892
FLATHEAD	9931.28	1230	30	1260	899	0.123851	0.003021	0.126872	0.090522
GALLATIN	2544.21	106	147	253	18	0.0416633	0.057778	0.099442	0.007075
GRANITE	1727.13	31	2	33	20	0.0179488	0.001158	0.019107	0.01158
JEFFERSON	1664.44	71	2	73	9	0.0426569	0.001202	0.043858	0.005407
LEWIS & CLARK	3490.84	250	119	369	33	0.071616	0.034089	0.105705	0.009453

Table AII.2. (Continued)

County (1900)	Area (Mi ²)	Adult Wolf	Pup Wolf	Total Wolf	Total Lion	Adult Wolf Density	Pup Wolf Density	Total Wolf Density	Total Lion Density
MADISON	4653.76	122	18	140	14	0.0262154	0.003868	0.030083	0.003008
MEAGHER	3441.21	613	243	856	29	0.1781351	0.070615	0.24875	0.008427
MISSOULA	4398.81	30	11	41	248	0.00682	0.002501	0.009321	0.056379
PARK	2767.80	405	58	463	67	0.1463254	0.020955	0.167281	0.024207
SILVER BOW	701.62	56	6	62	9	0.0798158	0.008552	0.088367	0.012828
SWEET GRASS	3049.91	342	184	526	16	0.1121344	0.06033	0.172464	0.005246
TETON	7492.09	250	788	1038	6	0.0333685	0.105178	0.138546	0.000801
VALLEY	13639.45	874	1192	2066	7	0.0640788	0.087394	0.151472	0.000513
YELLOWSTONE	5942.05	825	883	1708	0	0.1388409	0.148602	0.287443	0

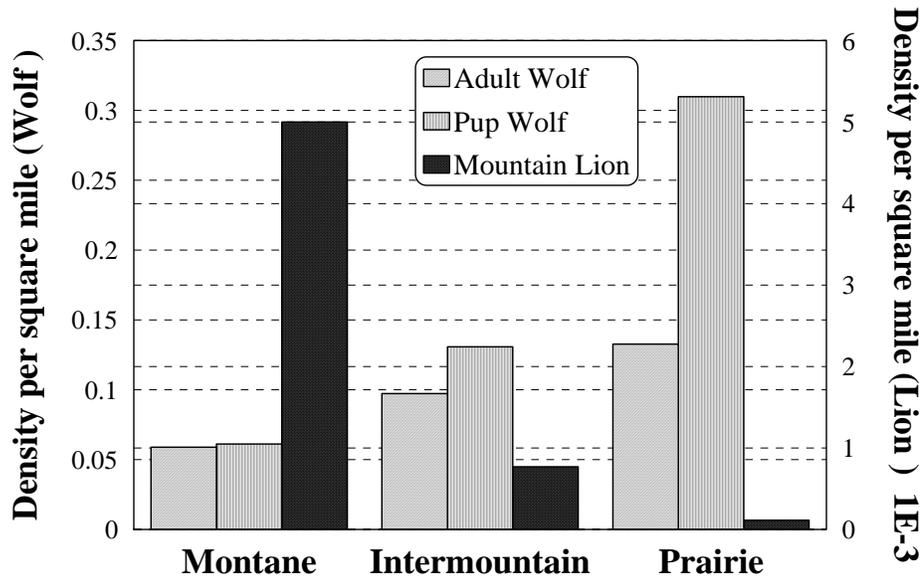


Figure AII.3. A comparison of the cumulative density of wolf and mountain lion bounty payments, 1990 - 1931, by ecoregion in Montana.

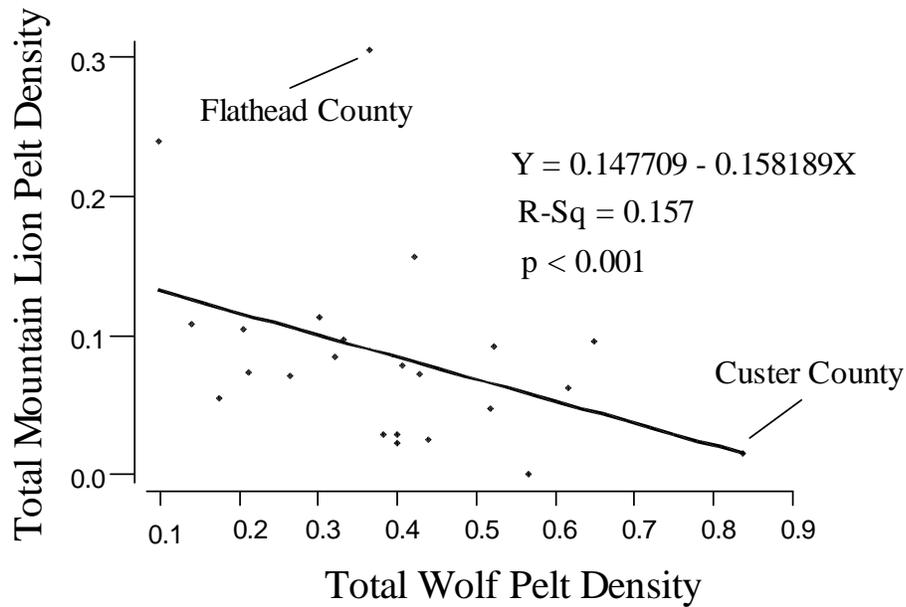


Figure AII.4. The relationship between density of total wolf pelts and lions pelts presented for bounty payment, 1900 - 1931, by county in Montana.

APPENDIX III

A GEOGRAPHICAL INFORMATION SYSTEM MODEL USED TO FORMULATE A TERRAIN RUGGEDNESS INDEX (TRI) USING ARC/INFO GRID SOFTWARE.

Based on 1:24000 maps, a terrain ruggedness index model (TRI) was computed with an Arc/Info geographical information system. The model derives a TRI value for each pixel of a 1 km digital elevation model using a “DOCELL” command and taking into account the sum change in elevation between any one pixel and its 8 neighboring pixels. The TRI values are then summed across any given area as displayed in the following example.

-1,-1	0,-1	1,-1
-1,0	0,0,	1,0
-1,1	0,1	1,1

Figure AIII.1. A grid diagram that depicts the model from which a terrain ruggedness index was calculated.

If each square above represents a pixel on a digital elevation model, then TRI = $Y = [\sum(x_{ij} - x_{00})^2]^{1/2}$ where, x_{ij} = elevation of each neighbor cell to cell (0,0).

The docell command is as follows:

```
DOCELL
```

```
    ssdiff:= ((sqr(el(0, 0) - el (-1, -1))) + (sqr (el (0, 0) - el (0, -1)))  
    + ... (sqr(el (0,0) - el (1, 1))).
```

```
    tri = srt (ssdiff)
```

```
end
```

where: ssdiff = temporary scalar, square feet.

el = name of elevation grid.

Table AIII.1. Terrain ruggedness index (TRI) values for 1995 hunting districts (HD) in Montana.

HD	TRI	HD	TRI	HD	TRI	HD	TRI
100	1132	285	810	404	101	530	134
101	939	290	189	405	159	540	304
102	632	291	676	406	134	560	982
103	914	292	789	410	178	570	215
104	1256	293	710	411	372	575	256
110	1021	300	788	412	466	580	503
120	806	301	1001	413	520	590	165
121	1358	302	893	415	915	600	96
122	1059	310	911	416	538	610	59
123	1194	311	557	417	138	620	97
124	1374	312	625	418	390	621	309
130	1085	313	1289	419	133	622	182
132	1163	314	1048	420	541	623	166
140	1258	315	537	421	412	630	102
141	1299	316	1019	422	588	631	229
150	1253	317	1309	423	644	632	162
151	1073	319	753	424	788	640	103
170	74	320	778	425	342	641	97

Table AIII.1 Continued,

HD	TRI	HD	TRI	HD	TRI	HD	TRI
200	1089	321	426	426	235	650	111
201	1096	322	589	427	906	651	114
202	1163	323	868	428	1187	670	120
203	1037	324	783	432	659	680	240
204	997	325	602	441	442	690	272
210	690	326	440	442	916	700	152
211	828	327	604	444	171	701	117
212	710	328	721	445	556	702	177
213	661	329	562	446	553	703	130
214	928	330	783	447	442	704	182
215	576	331	800	448	570	705	133
216	1040	332	721	449	483	818	720
240	1342	333	779	450	162	835	718
250	1137	340	551	452	638	839	571
260	251	341	632	454	447	843	634
261	774	360	934	455	910	850	777
270	840	361	626	471	160	870	960
280	1097	362	1095	500	165	880	540
281	792	393	571	502	294	890	647
282	440	400	98	510	617	891	496
283	993	401	145	511	238	892	830
284	376	403	130	520	1252		

APPENDIX IV

A self-administered mail questionnaire used for inquiry into the beliefs, attitudes, risk perception, and mountain lion population preferences of stakeholders in Montana, 1997.

MOUNTAIN LIONS IN MONTANA:

A Survey of Your Views



***Montana Fish,
Wildlife & Parks***

**PO Box 200701
Helena, MT 59620-0701**

MOUNTAIN LIONS IN MONTANA: A Survey of Your Views

A survey conducted by:
Montana Fish, Wildlife and Parks
1420 East Sixth Avenue
PO Box 200701
Helena, MT 59620-0701

**Your responses will remain confidential
and will never be associated with your name.**

This questionnaire is part of a study to assist wildlife managers with making decisions about mountain lions in Montana. Your views are very important to us and will make a difference in how lion management is conducted. Please complete this questionnaire at your earliest convenience, seal it, and drop it in any mailbox (no envelope is needed). Return postage has been provided. The questionnaire should take about 20 minutes to complete.

By completing and returning this questionnaire you will be entered in a drawing for a free one-year subscription to *Montana Outdoors*.

If you have questions regarding this survey, please write John McCarthy, Special Projects Coordinator, at the above address, or call him at (406) 444-2612.

We welcome you to use the inside, back cover of this questionnaire to record any additional comments about mountain lions.

THANK YOU FOR YOUR ASSISTANCE!

Printed on Recycled Paper

WILDLIFE AND YOU:

- 1. Montanans are involved with wildlife in many ways. Which of the following statements best describes your current level of interest and involvement?** (Please check **ONLY ONE** statement.)

- I am interested in wildlife, BUT I don't do much that is specifically related to wildlife.
- I am interested in wildlife AND I actively take part in wildlife related activities.
- I am NOT very interested in wildlife AND I don't do much that is specifically related to wildlife.
- I am NOT very interested in wildlife BUT for various reasons I am involved in wildlife-related activities.

- 2. The following is a list of some activities that bring people into contact with wildlife. Please indicate which of the following activities you, or members of your household, participate in regularly?** (Please check **ALL** statements that apply.)

	Yourself	Others in your household
a. Hike in the foothills or mountains	<input type="checkbox"/>	<input type="checkbox"/>
b. Jog in the foothills or mountains	<input type="checkbox"/>	<input type="checkbox"/>
c. Mountain bike in the foothills or mountains ..	<input type="checkbox"/>	<input type="checkbox"/>
d. Read about wildlife	<input type="checkbox"/>	<input type="checkbox"/>
e. Watch wildlife TV programs, videos, or movies	<input type="checkbox"/>	<input type="checkbox"/>
f. Observe or study wildlife outdoors	<input type="checkbox"/>	<input type="checkbox"/>
g. Work on a farm or ranch	<input type="checkbox"/>	<input type="checkbox"/>
h. Hunt big game	<input type="checkbox"/>	<input type="checkbox"/>
i. Hunt mountain lions	<input type="checkbox"/>	<input type="checkbox"/>
k. None of the experiences described above ...	<input type="checkbox"/>	<input type="checkbox"/>
l. Other activities: _____	<input type="checkbox"/>	<input type="checkbox"/>

MOUNTAIN LIONS AND YOU:**3. Before receiving this questionnaire, did you know that mountain lions live in Montana?**

[] Yes

[] No → *If you answered NO, please skip to question number 6 on the next page.***4. Please indicate which, if any, of the following types of interactions with mountain lions you or members of your household have experienced? (Please check [] ALL that apply.)**

	Yourself	Others in your household
a. Observed a mountain lion in the wild	[]	[]
b. Read or heard of a mountain lion being killed by authorities	[]	[]
c. Had a pet threatened or attacked by a mountain lion	[]	[]
d. Had livestock threatened or attacked by a mountain lion	[]	[]
e. Have been personally threatened by a mountain lion	[]	[]
f. Read or heard about pets being threatened or attacked by a mountain lion	[]	[]
g. Read or heard about livestock being threatened or attacked by a mountain lion	[]	[]
h. Read or heard about other people being threatened or attacked by a mountain lion	[]	[]
i. Know a friend or neighbor who had an encounter with a mountain lion	[]	[]
j. Hunted mountain lions	[]	[]
k. None of the experiences described above	[]	[]
l. Other types of experiences: _____		

5. How has the mountain lion population in your area of Montana changed during the past five years?

(Please check [] ONLY ONE of the following.)

- [] Decreased Greatly
 [] Decreased Somewhat
 [] Remained the Same
 [] Increased Somewhat
 [] Increased Greatly
 [] Don't Know

6. People in Montana have many different attitudes towards mountain lions. To what extent do you agree or disagree with each of the following statements? (Please circle the number that best represents your response to each statement.)

- 2 = Disagree Strongly - 1 = Disagree 0 = Neither Agree nor Disagree
 +2 = Agree Strongly +1 = Agree 9 = No Opinion

	Disagree Strongly				Agree Strongly	No Opinion
a. The presence of mountain lions is a sign of a healthy environment	-2	-1	0	+1	+2	9
b. Mountain lions help maintain deer populations in balance with their habitats ...	-2	-1	0	+1	+2	9
c. The presence of mountain lions <u>in Montana</u> increases my overall quality of life	-2	-1	0	+1	+2	9
d. The presence of mountain lions <u>near my home</u> increases my overall quality of life	-2	-1	0	+1	+2	9
e. Mountain lions <u>do not</u> compete with hunters for deer	-2	-1	0	+1	+2	9
f. Mountain lions should have the right to exist wherever they may occur	-2	-1	0	+1	+2	9
g. Mountain lions are an unacceptable threat to livestock	-2	-1	0	+1	+2	9

7. Encounters between mountain lions and people carry some level of risk to people, pets, or livestock. The following questions are designed to help us better understand your opinions about lion-human encounters in Montana.

On a scale of 1-to-5 please circle the number between the two words in each row that most closely represents your opinion. DK = Don't Know.

- a. Are encounters between mountain lions and people new and novel, or have they been occurring for a long time in Montana?**

A new event 2 3 4 An old event DK
1

- b. Are lion-human encounters increasing or decreasing in Montana?**

Increasing Decreasing
1 2 3 4 5 DK

- c. To what extent do you believe that you personally are at risk from mountain lions in the areas that you live, work and recreate?**

I am at no risk I am at great risk
1 2 3 4 5 DK

- d. Are the risks associated with mountain lions something society can learn to live with, or are the risks something people will be unable to learn to live with over time?**

Able to learn to live with the risks Unable to live with the risks
1 2 3 4 5 DK

- e. Are the risks from mountain lions generally accepted voluntarily -- that is, can people make choices about being exposed to the risks?**

Risks accepted voluntarily Risks accepted Involuntarily
1 2 3 4 5 DK

- f. Are the risks associated with having mountain lions in Montana understood by experts?**

Not well understood Well understood
1 2 3 4 5 DK

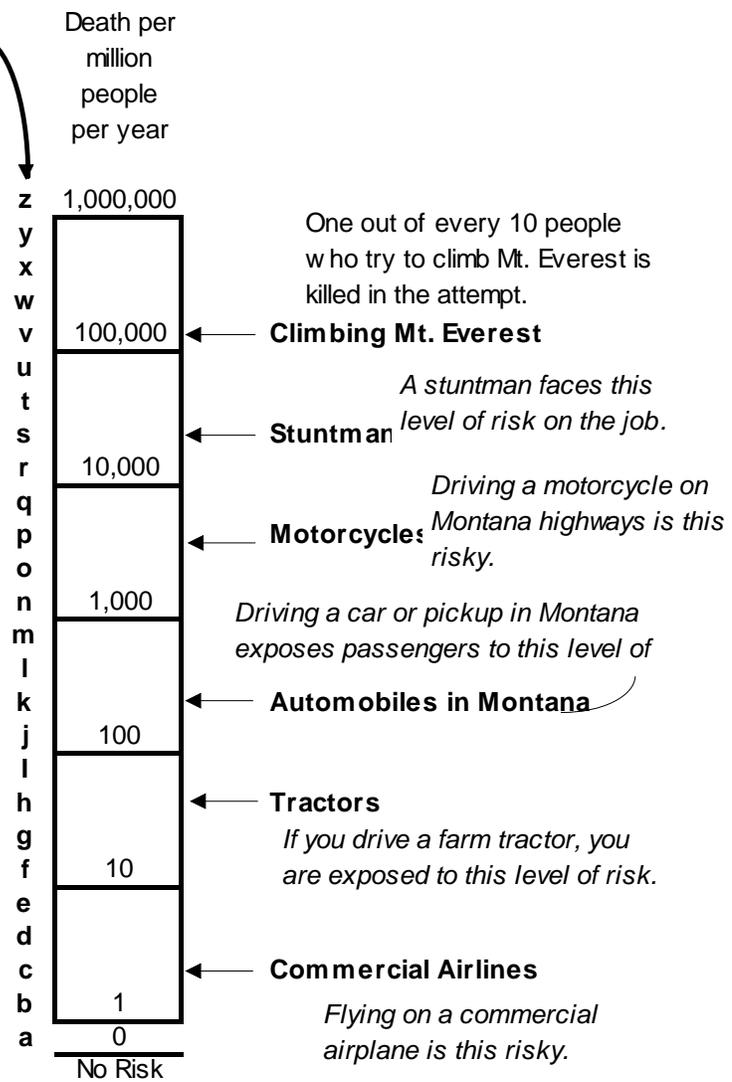
- g. Are the people who benefit from mountain lions the same people who are exposed to the potential risks of living with lions?**

Benefits and risks are matched Benefits and risks are mismatched
1 2 3 4 5 DK

8. This question is designed to help us better understand your perceptions about the possibility of Montanans suffering injury, or even death, from mountain lion attacks. Please circle a single letter along the left side of the column below that corresponds to the relative risk you perceive mountain lions pose to people in Montana. For comparison, risks from commonplace hazards are listed on the right side of the column.

Example: A person was asked to indicate what the risk is from handgliding in the Rocky Mountains. She circled the letter “q” indicating that she believes handgliding is slightly more risky than riding motorcycles, but somewhat less risky than being a stuntman.

Please circle a single letter in this column that corresponds to the relative risk you perceive that mountain lions pose to people in



9. Many different feelings exist towards mountain lions. Generally, which one of the following statements best reflects how you feel about lions living in areas where you live, work or recreate?

(Please check [] only ONE of the following statements.)

- I enjoy having mountain lions AND I do not worry about problems they may cause.
- I enjoy having mountain lions BUT I do worry about problems they may cause.
- I do not enjoy having mountain lions AND I do worry about problems they may cause.
- I do not enjoy having mountain lions BUT I do not worry about problems they may cause.
- I have no particular feelings about mountain lions regardless of problems caused or not caused by them.

YOUR PREFERENCE FOR MOUNTAIN LION POPULATIONS:

10a. Wildlife managers would like to know whether you want the mountain lion population in your area to increase, decrease or remain at its current level over the next five years.

(Please check [] only ONE of the following statements.)

- Decrease Greatly
- Decrease Somewhat
- Remain at its current level
- Increase Somewhat
- Increase Greatly
- No Opinion

10b. How important is it to you personally that the mountain lion population trend match your response to question 10a?

(Please check [] only ONE of the following statements.)

- Very Unimportant
- Somewhat Unimportant
- Neither Important nor Unimportant
- Somewhat Important
- Very Important
- No Opinion

MOUNTAIN LION MANAGEMENT:

During a recent study on mountain lion management in Montana, numerous options for managing lions were proposed by citizens. Whereas Fish, Wildlife and Parks is not currently considering implementation of the following proposals, we wish to know how acceptable these potentially controversial actions would be to you.

11. How acceptable would it be to you if mountain lion hunting was discontinued in your area of Montana?

(Please check [] only ONE of the following statements.)

- Very Unacceptable
- Somewhat Unacceptable
- Neither Acceptable nor Unacceptable
- Somewhat Acceptable
- Very Acceptable
- No Opinion

12. How acceptable would it be to you if livestock growers were reimbursed for documented losses of livestock to mountain lions? The following is a list of suggested sources of money for reimbursement.

(Please circle the number that best represents how acceptable it would be to you for each source listed below to make reimbursement payments.)

- 2 = Very Unacceptable
- 1 = Somewhat Unacceptable
- 0 = Neither Acceptable nor Unacceptable
- +1 = Somewhat Acceptable
- +2 = Very Acceptable
- 9 = No Opinion

	Very <u>U</u> nacceptable		Neither		Very Acceptable	
a. Montana Fish, Wildlife and Parks, using money from the sale of hunting licenses	-2	-1	0	+1	+2	9
b. State of Montana, using general tax money	-2	-1	0	+1	+2	9
c. Environmental organizations, using private donations	-2	-1	0	+1	+2	9

- 20. Please use the space below for any additional comments you wish to make about mountain lions or lion management in Montana.**

If you wish to receive a summary
of this study, please check this box

TO RETURN THE SURVEY:

**Simply seal it and drop in any mailbox.
Return postage is provided.**

THANK YOU FOR YOUR TIME AND HELP!

LITERATURE CITED

- Ashman, D.L., G.C. Christensen, M.L. Hess, G.K. Tsukamoto, and M.S. Wickersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife Technical Bulletin. 75 pp.
- Anderson, A.E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division Wildlife Special Report No. 54. 91pp.
- Aune, K., and P. Schladweiler. 1994. Wildlife laboratory annual report. Montana Fish, Wildlife and Parks. Helena, MT.
- Bath, A.J. 1996. Increasing the applicability of human dimensions research to large predators. *Journal Wildlife Research* 1(2):215-220.
- _____, and T. Buchanan. 1989. Attitudes of interest groups in Wyoming toward wolf restoration in Yellowstone National Park. *Wildlife Society Bulletin* 17:519-525.
- Beasom, S.L., E.P. Wiggers, and J.R. Giardino. 1983. A technique for assessing land surface ruggedness. *Journal Wildlife Management*. 47(4):1163-1166.
- Beier, P. 1991. Mountain lion attacks on humans in the United States and Canada. *Wildlife Society Bulletin* 19: 403-412.
- Berger, J., and J.D. Wehausen 1991. Consequences of a mammalian predator-prey disequilibrium in the Great Basin Desert. *Conservation Biology* 2:224-248.
- Bernstein, P.L. 1996. *Against the Gods: the remarkable story of risk*. John Wiley & Sons. New York.
- Bissonette, J.A. 1997. Scale-sensitive properties: historical context, current meaning. Pp 3-31 in J.A. Bissonette, editor *Wildlife and landscape ecology: Effects of pattern and scale*. Springer-Verlag, New York.
- Bjorge, R.R. and J.R. Gunson. 1983. Wolf predation of cattle on the Simonette Rivers pastures in northwestern Alberta. Pp. 106-111 in Harrington, F.H. and P. Paquet (Eds.) *Wolves of the world: Perspectives of behavior, ecology, and conservation*.

- Bolgiano, C. 1995. Mountain lion: an unnatural history of pumas and people.: Stackpole, Mechanicsburg, PA.
- Botkin, D. 1990. Discordant harmonies: a new ecology for the twenty-first century. Oxford University Press, New York. 241 pp.
- Braun, C.E., editor 1991. Symposium on mountain lion-human interactions. Colorado Division of Wildlife, Denver.
- Bright, A.D., and M.J. Manfredo. 1996. A conceptual model of attitudes towards natural resource issues: a case study of wolf reintroduction. *Human Dimensions of Wildlife* 1:1-21.
- Brown, T.L., D.J. Decker, and N.A. Connelly. 1989. Response to mail surveys on resource-based recreation topics: a behavioral model and an empirical analysis. *Leisure Science* 11:99-110.
- Bunnell, F.L., and D.E.N. Tait. 1980. Bears in models and reality -- implications to management. Pp 15-23 *in* Bears -- their biology and management. Bear Biology Association Series 4. 375pp.
- Bureau of Business and Economic Research. 1995. Outlook: constructing the future of Montana's economy. School of Business Administration, Univ. MT, Missoula. 47pp.
- Burgman, M.A., S. Ferson, and H.R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, New York, NY 314pp.
- Cahalane, V.H. 1964. A preliminary study of the distribution and numbers of cougar, grizzly, and wolf in America. New York Zoological Society, New York.
- Casswell, H. 1989. Matrix population models. Sinauer Publishers, Sunderland, MA. 328 pp.
- Caughley, G. 1977. Analysis of vertebrate populations. Wiley & Sons, New York. 234pp.
- _____, and A.R.E. Sinclair. 1994. Wildlife ecology and management. Blackwell Scientific Publications, Boston. 334pp.

- Center for National Policy. 1992. Montana: a steady state in transition. A report to the Liz and Art Ortenberg Foundation. Center for National Policy, Washington, DC. 25 pp.
- Clark, T.W. 1993. Creating and using knowledge for species and ecosystem conservation: science, organizations and policy. *Perspectives in Biology and Medicine*. 36(3)497-525.
- _____, A.P. Curlee, and R.P. Reading. 1996. Crafting effective solutions to the large carnivore conservation problem. *Conservation Biology*. 10:940-948.
- Conway, A.J., and P.S. Goodman. 1989. Population characteristics and management of the black rhinoceros *Diceros bicornis minor* and white rhinoceros *Ceratotherium simum simum* in Ndumu Game Reserve, South Africa. *Biological Conservation* 47:109-122.
- Coues, E. 1893. History of the expedition under the command of Lewis and Clark, Volume I. Dover Publishing Co. NY
- Craven, S.R., D.J. Decker, W.F. Siemer, and S.E. Hygnstrom. 1992. Survey use and landowner tolerance in wildlife damage management. *Trans. N. Am. Wildlife and Natural Resources Conference* 57:75-88.
- Crowder, L.B., D.T. Crouse, S.S. Heppell, and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4:437-445.
- Curtis, P.D., and J.R. Hauber. 1997. Public involvement in deer management decisions: consensus versus consent. *Wildlife Society Bulletin* 25:399-403.
- Decker, D. J. 1994. What are we learning form human dimensions studies in controversial wildlife situations? Occasional Papers Series No. 21, Colorado Division of Wildlife, Denver.
- _____, T.L. Brown, and G.F. Mattfeld. 1987. Integrating social science into resource management: barriers and limitations. Pp 83-92 in M.L. Miller, R.P. Gale, and P.J. Brown, editors *Social science in natural resource management systems*. Westview Press, Boulder, CO. 265 pp.

- _____, and L.C. Chase. 1998. Human dimensions of living with wildlife -- a management challenge for the 21st century. *Wildlife Society Bulletin* 25:788-795.
- _____, N.A. Connelly, J.W. Enck, G.A. Pomerantz, K.G. Purdy, and W.F. Siemer. 1992. Toward a comprehensive paradigm of wildlife management: integrating the human and biological dimensions. Pages 33-54 in W.R. Mangun, editor *American fish and wildlife policy: the human dimension*. Southern Illinois Press, Carbondale.
- _____, C.C. Krueger, R.A. Baer, B.A. Knuth, and M.E. Richmond. 1996. From client to stakeholders: a philosophical shift for fish and wildlife management. *Human Dimensions of Wildlife Management* 1(1): 70-82
- _____, and J. Lipscomb. 1991. Toward an organizational philosophy about integrating biological and human dimensions in management. *Human Dimensions Perspectives Series No. 1, Occasional Papers*, Colorado Division of Wildlife, Denver. 3pp.
- _____, and K.G Purdy. 1988. Towards a concept of wildlife acceptance capacity in wildlife management. *Wildlife Society Bulletin* 16:53-57.
- deLeon, P. 1994. Reinventing the policy process: three steps back to the future. *Policy Sciences* 27:77-95.
- Dillman, D.A. 1978. *Mail and telephone surveys: the total design method*. John Wiley and Sons., New York. 325 pp.
- Eagly, A.H. and S. Chaiken. 1993.. *The psychology of attitudes*. New York: Harcourt Brace Jovanovich Publishers.
- Eaton, R.L. 1973. The status, management and conservation of the cougar in the United States. *World's Cats* 1:68-89.
- Escos, J., C.L. Alados, and J. Emlen. 1994. Application of the stage-projection model with density-dependence fecundity to the population dynamics of Spanish Ibex. *Canadian Journal of Zoology* 72:731-737.
- Estes, J.A. 1996. Predators and ecosystem management. *Wildlife Society Bulletin* 24:390-396.

- Fazio, J.R. and L.A. Belli. 1977. Characteristics of nonconsumptive wildlife users in Idaho. *Trans. North American Wildlife and Natural Resources Conference* 42:117-28.
- Fiorino, D.J. 1989. Technical and democratic values in risk analysis. *Risk Analysis* 9:293-299.
- Fuller, T.K., and D.B. Kittredge, Jr. 1996. Conservation of large forest carnivores. Pp 139-164 in *Conservation of faunal diversity in forested landscapes*. DeGraaf and R.I. Miller, editors Chapman and Hall, London.
- Gassaway, W.C., R.O. Stephenson, J.L. Davis, P.E.K. Shepard, and O.E. Burris. 1983. Interrelationships of wolves, prey and man in interior Alaska. *Wildlife Monographs* 84. 50 Pp.
- Genoways, H.H., and P. W. Freeman. 1996. A recent record of mountain lion in Nebraska. *Prairie Naturalist*. 28:143-145.
- Gill, R. B. 1996. The wildlife professional subculture: the case of the crazy aunt. *Human Dimensions of Wildlife Management* 1:60-69.
- Gittleman, J.L., and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology* 10:57-63.
- Gonyea, W.J. 1976. Adaptive differences in body proportions of large felids. *Acta Anatomica*. 96:81-96.
- Goodman, D. 1980. Demographic intervention for closely managed populations. Pp 171-195 in Soule', M.E. and B.A. Wilcox, editors *Conservation biology: an evolutionary-ecological perspective*. Sinauer, Sunderland, MA.
- Goodwin, P., and G. Wright. 1991. *Decision analysis for management judgment*. John Wiley & Sons. New York.
- Gregory, R., and R.L. Keeney. 1994. Creating policy alternatives using stakeholder values. *Management Science* 40:1035-1048.

- Grossman, W-D. 1993. Integration of social and ecological factors: dynamic area models of subtle human influences on ecosystems. Pp. 229-245 *in* Humans as components of ecosystems: the ecology of subtle human effects and populated areas. M.J. McDonnell and S.T.A. Pickett editors Springer-Verlag, New York.
- Gruell, G.B. 1983. Fire and vegetation trends in the northern Rockies: interpretations from 1871-1982 photographs. USDA Forest Service. Intermountain Forest and Range Experiment Station, Ogden, UT. General Technical Report INT-158.
- Guynn, D.E., and M.K. Landry. 1997. A case study of citizen participation as a success model for innovative solutions for natural resource problems. *Wildlife Society Bulletin* 25:392-398.
- Hansen, K. 1992. Cougar: the American lion. Northland Publishing Company, Flagstaff, AZ.
- Harveson, L.A. 1997. Ecology of a mountain lion population in southern Texas. Ph.D. Dissertation, Texas A&M University, College Station, TX.
- Hemker, T.P, F.G. Lindzey, and B.B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah, *Journal of Wildlife Management* 47:1275-1284.
- Heppell, S.S., J.R. Walters, and L.R. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. *Journal of Wildlife Management* 58:479-487.
- Hook, R., and W. Robinson. 1982. Attitude of Michigan citizens toward predators. Pp 382-386 in Harrington, F.H. and P. Paquet (Eds.) *Wolves of the world: Perspectives of behavior, ecology, and conservation*. Noyes Publications, Park Ridge, NJ.
- Hornocker, H.G. 1969. Winter territoriality in mountain lions. *Journal Wildlife Management*. 33(3):457-464.
- _____. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* No. 21.

- _____. 1976. The possible influence of mountain lion on mule deer populations. Pp 107-109 in G.W. Workman and J.B. Low, editors Mule deer decline in the West: a symposium. Utah State University, Utah Agricultural Experiment Station, Logan. 134 pp.
- _____. 1995. Cougar management: what lies behind us, what lies ahead. Proceedings. of Annual Conference Western Association of Fish and Wildlife Agencies. July 19, 1995, Big Sky, MT.
- _____, K. Murphy, G.S. Felzein, and S.E. Relyea. 1992. Ecology of the mountain lion in Yellowstone. Progress Report No. 5. Hornocker Wildlife Research Institute. Moscow, Idaho. 39p.
- Hunter, M.D., and P.W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 734-732.
- Iriarte, J.A., W.L. Franklin, W.E. Johnson, and K.H. Redfords. 1990. Geographic variation of food habits and body size of American puma. *Oecologia* 85:185-190.
- Issac, S., and W.B. Michael. 1981. Handbook in research and evaluation for education and behavior sciences. EDITS Publ., San Diego, CA 234pp.
- Jackson, P., and K. Nowell. 1996. Problems and possible solutions in management of felid predators. *Journal of Wildlife Research* 1:304-314.
- Jordan, C.F. and C. Miller. 1996. Scientific uncertainty as a constraint to environmental problem solving : large scale ecosystems. Pp 91- in Scientific uncertainty and environmental problem solving, J. Lemons editor Blackwell Science, Cambridge, MA.
- Keiter, R.B., and H. Locke. 1996. Law and large carnivore conservation in the Rocky Mountains of the U.S. and Canada. *Conservation Biology* 10:1003-1012.
- Kellert, S.R., 1983. Affective, cognitive, and evaluative perceptions of animals. Pp. 241-267 in Altman, I. and J. Wohlwill, editors. Behavior and the natural environment. New York: Plenum.

- _____. 1985. Public perceptions of predators, particularly the wolf and coyote. *Biological Conservation* 31:169-189.
- _____, and J.K. Berry. 1981. Knowledge, affection and basic attitudes towards animals in American society. Springfield, VA: National Technical Information Service. PB-81-173106.
- _____, M. Black, C.R. Rush, and A.J. Bath. 1996. Human culture and large carnivore conservation in North America. *Conservation Biology* 10:977-990.
- Kenney, R.L. 1995. Understanding life-threatening risks. *Risk Analysis* 15:627-637.
- Kenney, J.S., J.L.D Smith, A.M. Starfield, and C.W. McDougal. 1995. The long-term effects of tiger poaching on population viability. *Conservation Biology* 9:1127-1133.
- Kleiman, D.G. and J.F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behavior* 21:637-659.
- Kim, J.O., and C.W. Muller. 1978. Introduction to factor analysis: what it is and how to do it. Sage Publ., Beverly Hills, CA. 80pp,
- Knuth, B.A. and L.A. Nielsen. 1989. Social and institutional performance indicators for wildlife and fishery resource management systems. *Society and Natural Resource Management* 2:329-344.
- _____, R.J. Stout, W.F. Siemer, D.J. Decker, and R.C. Stedman. 1992. Risk management concepts for improving wildlife population decisions and public communication strategies. *Transactions 57th North American Wildlife and Natural Resources Conference* pp. 63-74.
- Kunkel, K. and D.H. Pletscher. 1994. Wolf ecology project. Unpublished progress report. University of Montana, Missoula.
- Laing, S.P. 1988. Cougar habitat selection and spatial use patterns in southern Utah. MS Thesis, University of Wyoming, Laramie. 68 pp.

- _____, and F.G. Lindzey. 1991. Cougar habitat selection in south-central Utah. Pp 27-37 in C.S. Braun editor Proceedings. Symposium Mountain lion-human Interactions. Denver, CO.
- _____. 1994. Patterns of replacement of resident cougars in southern Utah. *Journal of Mammalogy* 74:1056-1058.
- Lindzey, F.G. 1987. Mountain lion. pp. 657-668 in Nowak, M. et al. editors Wild furbearer management and conservation in North America. Ontario Trappers Association, Toronto. 1150pp.
- _____, B.B Ackerman, D. Barnhurst, T. Becker, T.P. Hemker, S.P. Laing, C. Mecham, and W.D. Van Sickle. 1989. Boulder-Escalante cougar project: final report. Utah Division Wildlife Research, Salt Lake. 92 pp.
- _____, W.D. Van Sickle, and S.P. Laing. 1992. Cougar population response to manipulation in southern Utah. *Wildlife Society Bulletin* 20:224-227.
- _____, B.B. Ackerman, D. Barnhurst, T.P. Hemker, and S.P. Laing. 1994. Cougar population dynamics in southern Utah. *Wildlife Society Bulletin* 58:619-624.
- Litvaitis, J.A., J.F. Beltran, M. Delibes, S. Moreno, and R. Villafuerte. 1996. Sustaining felid populations in human-dominated landscapes. *Journal Wildlife Research* 1(3):292-296.
- Llewellyn, L.G. 1978. Who speaks for the timber wolf? *Transaction North American Wildlife and Natural Resource Conference* 43:442-452.
- Logan, K.A. 1983. Mountain lion population and habitat characteristics in the Big Horn Mountains of Wyoming. MS Thesis. Univ. of Wyoming, Laramie. 101 pp.
- _____, and L.L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildlife Society Bulletin* 13:257-262.
- _____, L.L. Sweanor, T.K. Ruth, and M.G. Hornocker. 1996. Cougars of the San Andres Mountains. Final Report, Federal Aid in Wildlife Restoration Project W-128-R, New Mexico Game and Fish, Santa Fe.
- Lopez, B.H. 1987. *Of wolves and men*. Scribner's and Sons, New York.

- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17, 36.
- L'vovich, M.I., and G.F. White. 1990. Use and transformation of terrestrial water systems. Pp 235-252 in B.L. Turner et al., editors. *The Earth as transformed by human action: Global and regional changes in the biosphere over the past 300 years*. Cambridge Univ. Press, UK.
- Mackie, R.J., D.F. Pac, K.L. Hamlin, and G.L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. *Montana Fish, Wildlife and Parks*, Helena. 181pp.
- Macnab, J. 1985. Carrying capacity and other related slippery shibboleths. *Wildlife Society Bulletin* 13:403-410.
- Mallows, C.L. 1973. Some comments on C_p . *Technometrics* 15:661-675.
- Manfredo, M.J., D.J. Decker, and M.D. Duda. *in press*. What is the future for human dimensions of wildlife?
- Marschall, E.A., and L.B. Crowder. 1996. Assessing population responses to multiple anthropogenic effects: a case study with brook trout. *Ecological Application* 6:152-167.
- McCall, K., and J. Dutcher. 1992. *Cougar: ghost of the Rockies*. Sierra Club Books, San Francisco, CA.
- McClelland, G.H. W.D. Schulze, and B. Hurd. 1990. The effects of risk beliefs on property values: a case study of a hazardous waste site. *Risk Analysis* 10(4):485-497.
- McCullough, D.R. 1996. Spatially structured populations and harvest theory. *Journal of Wildlife Management* 60:1-9.
- _____, and R. Barrett editors 1992. *Wildlife 2001: populations*. Elsevier Applied Sciences, New York, NY.
- McDonnell M.J., and S.T.A. Pickett. 1993. *Humans as components of ecosystems: the ecology of subtle human effects and populated areas*. Springer-Verlag, New York.

- McNab H.W. and P.E. Avers, comps. 1994. Ecological subregions of the United States: Section descriptions. Admin. Publ. WO-WSA-5. USDA Forest Service. Washington, D.C. 267 pp.
- Meffe, G.K. and S. Viederman. 1995. Combining science and policy in conservation biology. *Wildlife Society Bulletin* 23(3):327-332.
- Merkhofer, M. W. 1987. Decision science and social risk management. D. Reidel Publ. Co., Boston, MA. 330 pp.
- Miller, S.D. and D.D. Everett, editors 1986. Cats of the world: biology, conservation and management. National Wildlife Federation, Washington, D.C.
- MINITAB, Inc. 1996. MINITAB release 11 for Windows reference manual. MINITAB, Inc. State College, PA.
- Montana Agricultural Statistics and Reporting Service. 1995. Montana livestock inventory: Montana state historical series. Montana Department of Agriculture. Helena.
- Moore, C.M. 1987. Group techniques for idea building. Applied Social Research methods, Series No. 9. Sage Publ., Newbury Park, CA. 143pp.
- Murphy, K. 1983. Characteristics of a hunted population of mountain lions in western Montana. MS Thesis, University of Montana, Missoula. 48pp.
- Mussehl, T.W., and F.W. Howell. 1971. Game management in Montana. Montana Fish and Game Department, Helena. 238 pp.
- Nero, R.W., and R.E. Wrigley. 1977. Status and habits of cougar in Manitoba. *Canadian Field Naturalist* 91:28-40.
- Nichols, J.D., G.L. Hensler, and P.W. Sikes, Jr. 1980. Demography of the Everglade kite: implications for population management. *Ecological Modeling* 9:215-232.
- Noss, R.F. H.B. Quigley, M.G. Hornocker, T. Merrill, and P.C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* (10)4:949-963.

- Nowak, R.M. 1976. The cougar in the United States and Canada. U.S. Fish and Wildlife Service., Washington D.C. 190pp.
- Nowell, K. and P. Jackson editors 1996. Wild cats: status survey and conservation action plan. International Union Conservation Of Nature and Natural Resources. Gland, Switzerland.
- Olsen, P.D. 1992. Worskshop welcome and overview. P.2 in Braun, C.E., editor Symposium on mountain lion-human interactions. Colorado Division of Wildlife, Denver. 114 pp.
- Ottway, H. 1992. Public wisdom, expert fallibility: toward a contextual theory of risk. Pp 215-228 in Social theories of risk. Krimsky, S. And D. Golding, editors Praeger, Westport, CT.
- Padley, W.D., editor. 1997. Proceedings of the fifth mountain lion workshop: 27 February - 1 March 1996, San Diego, CA. 135 pp.
- Paquet, P.C., and A. Hackman. 1995. Large carnivore conservation in the Rocky Mountains: a long-term strategy for maintaining free-ranging and self-sustaining populations of carnivores. World Wildlife Fund Canada, Toronto, Ontario.
- Pickett, S.T.A. and M.J. McDonnell. 1993. Humans as components of ecosystems: a synthesis. Pp 310-316 in McDonnell M.J. and S.T.A. Pickett. Humans as components of ecosystems: the ecology of subtle human effects and populated areas. Springer-Verlag, New York.
- Pielou, E.C. 1991. After the ice age: the return of life to glaciated North America. University of Chicago Press. 366 pp.
- Pomerantz, G.A. C. Ng, and D.J. Decker. 1986. Summary of research on human tolerance of wildlife damage. Natural Resources Research and Extension Series No. 25. Department Natural Resources, Cornell University, Ithaca, NY. 42 pp.
- Pickett, S.T.A. and M.J. McDonnell. 1993. Humans as components of ecosystems: a synthesis. Pp 310-316 in McDonnell M.J. and S.T.A. Pickett. Humans as components of ecosystems: the ecology of subtle human effects and populated areas. Springer-Verlag, New York.

- Renn, O. 1992. Concepts of risk: a classification. Pp. 53-82 *in* Krimmsky, S., and D. Golding. *Social theories of risk*. Praeger Publ. Westport, CT. 412 pp.
- Riebsame, W.E. 1997. *Atlas of the new West: portrait of a changing region*. W.W. Norton and Co. 1997. New York.
- _____, W.E., W.J. Parton, K.A. Galvin, I.C. Burke, L. Bohren, R. Young, and E. Knop. 1994. Integrated modeling of land use and cover change: a conceptual scheme for applying an integration strategy to agricultural land use on the Great Plains. *Bioscience* 44(5):350-356.
- Riley, S.J. 1992. *Cougars in Montana: a review of biology and management and a plan for the future*. Unpublished. Manuscript, Montana Dept. Fish, Wildlife and Parks, Helena, 38p.
- _____, and K. Aune. 1997. An evaluation of lion-human interactions in Montana. *Trans. Western States Cougar Workshop*, San Diego, CA.
- _____, R.D. Mace, and M. Madel. 1994. Translocation of nuisance grizzly bears in northwestern Montana. *International Conference on Bear Research and Management* 9(1):567-573.
- Roseberry, J.L., and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. *Wildlife Monographs* No. 117.59 pp.
- Ross, P.I., and M.G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. *Journal of Wildlife Management* 56:41-426.
- _____, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Canadian Journal Zoology* 75(5):771-775.
- Russell, K.R. 1978. Mountain lion. Pp 207-225 *in* Schmidt, J.L., and D.L. Gilbert, editors. *Big game of North America: ecology and management*. Stackpole Books, Harrisburg, PA. 494pp.

- Schrader-Frechette, K.S., and E.D McCoy. 1993. Method in ecology. Cambridge University Press, New York. 328 pp.
- Seidensticker, J.C. IV, M.G. Hornocker, W.V. Wiles, and J.P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monograph 35. 60 pp.
- Siemer, W.F. and D.J. Decker, 1991. Human tolerance of wildlife damage: synthesis of research and management implications. Human Dimensions Research Unit Series No. 91-7. Department Natural Resources, Cornell University, Ithaca, NY. 24 pp.
- Slobodkin, L.B., and D.E. Dykhuizen. 1991. Applied ecology, its practice and philosophy. Pp 63-70 in Cairns, J. and T.V. Crawford, editors Integrated environmental management. Lewis Publishers, Inc. Chelsea, MI.
- Slovic, P. 1987. Perception of risk. Science 236:280-285.
- _____. 1993. Perceived risk, trust, and democracy. Risk Analysis 13:675-682.
- _____, B. Fischhoff, and S. Lichtenstein. 1981. Perceived risk: psychological factors and social implications. in F. Warner and D.H. Slater, editors. The assessment and perception of risk. Royal Society, London, UK.
- Smallwood, K.S., and E.L. Fitzhugh. 1995. A track count for estimating mountain lions (*Felis concolor californica*) population trend. Biology Conservation 71(3):251-259.
- Smil, V. 1985. Carbon-nitrogen-sulfur human interference in grand biospheric cycles. Plenum Press, New York.
- _____. 1990. Nitrogen and phosphorous. Pp 423-436 in B.L. Turner et al Eds. The Earth as transformed by human action: Global and regional changes in the biosphere over the past 300 years. Cambridge University Press, UK.
- Spreadbury, B.R., K. Musil, J. Musil, C. Kaisner, and J. Koviak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962-969.

- Starfield, A.M. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61:261-270.
- _____, J.D. Shiell, and G.L. Smuts. 1981. Simulation of lion control strategies in a large game reserve. *Ecological Modeling* 13:17-28.
- Stevens, W.K. 1994. Survival of the big cats bring conflict with man. *New York Times*, August 2, Pp. C1 & C4.
- Stout, R.J., D.J. Decker, B.A. Knuth, J.C. Proud, and D.H. Nelson. 1996. Comparison of three public involvement approaches for stakeholder input into deer management decisions: a case study. *Wildlife Society Bulletin* 24:312-317.
- _____, R.C. Stedman, D.J. Decker, and B.A. Knuth. 1993. Perceptions of risk from deer-related vehicle accidents: implications for public preferences for deer herd size. *Wildlife Society Bulletin* 21:237-249.
- Sunquist, M.E., and F.C. Sunquist. 1989. Ecological constraints on predation by large felids. Pp 283-301 *in* Gittlemen, J.L., editor *Carnivore behavior, ecology, and evolution*. Cornell University Press.
- Sweanor, L. 1990. Mountain lion social organization in a desert environment. MS Thesis. University of Idaho, Moscow. 172 pp.
- _____, K Logan, and M. Hornocker. 1996. Cougar social organization. Chapter 4 in Logan, K.A, L.L. Sweanor, T.K. Ruth, and M.G. Hornocker. 1996. *Cougars of the San Andres Mountains. Final Report, Federal Aid in Wildlife Restoration Project W-128-R, New Mexico Game and Fish, Santa Fe.* 280 pp.
- Tanner, J.T. 1975. The stability and intrinsic growth rates of prey and predator populations. *Ecology* 56:855-867.
- Thompson, J.G. 1992. Addressing the human dimensions of wolf reintroduction: an example using estimates of livestock depredation and costs of compensation. *Society and Natural Resources* 6:165-179.
- Thorndale, W., and W. Dollarhide. 1987. Map guide to the U.S. Censuses, 1790-1920. Genealogical Publishing Company, Baltimore, MD. 420 pp.

- Tucker, P. and D.H. Pletscher. 1989. Attitudes of hunters and residents toward wolves in northwestern Montana. *Wildlife Society Bulletin* 17:509-514.
- Turner, M.G. 1987. land use changes and net primary production in the Georgia, USA, landscape: 1935-1982. *Environmental Management* 11:237-247.
- _____, R.H. Gardner, and R.V. O'Neill. 1995. Ecological dynamics at broad scales. *Bioscience (Supplement 30 on Science and Biodiversity Policy):S-29-S-35*.
- USDC. 1994. Interim Census. Div. of Economics and Statistics, Bureau of the Census, US Dept. of Commerce, Washington, D.C. CD ROM data.
- USGS. 1991. Estimated use of water in the United States in 1990. National Circular 1081.
- Vaughan, T.A. 1978. *Mammology*. W.B. Saunders Co., Philadelphia. 522 pp.
- Wagner, F.H. 1978. Effects of livestock grazing and the livestock industry on wildlife. *in* Brokaw, H., editor. *Wildlife in America*. Council on Environmental Quality. Washington, D.C.
- Waller, D.M., and W.S. Alverson. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 217-226.
- Weaver, J.L., P.C. Paquet, and L.F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10:964-976.
- Weaver, R.A., and L.W. Sitton. 1978. Changing status of mountain lion in California and livestock depredation problems. *Proceedings Vertebrate Pest Conference* 8:214-219.
- Williams, J.S. 1992. Ecology of mountain lions in the Sun River area of northern Montana. MS Thesis. Montana State University, Bozeman.
- _____, J.J. McCarthy, and H.D. Picton. 1995. Cougar habitat use and food habits on the Montana Rocky Mountain Front. *Intermountain Journal Sciences* 1(1):16-28.

Wisdom, M.J., and L.S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *Journal of Wildlife Management* 61:302-312.

Young, S.P., and E.A. Goldman. 1946. *The puma: Mysterious American cat*. American Wildlife Institute, Washington, DC.

Zar, J. 1984. *Biostatistical analysis*, 2nd Ed. Prentice-Hall.

Zechauser, R.J., and W.K. Viscusi. 1990. Risk within reason. *Science* 248: 559-564.

Zinn, H.C. and M.J. Manfredo. 1996. Societal preferences for mountain lion management along Colorado's front range. HDNRU Rep. No. 28, Colorado State Univ., Ft. Collins.