Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Metapopulation Dynamics, and Population Recover

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COUGAR EXPLOITATION LEVELS IN UTAH: IMPLICATIONS FOR
DEMOGRAPHIC STRUCTURE, METAPOPULATION DYNAMICS, AND
POPULATION RECOVERY

by

David C. Stoner

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Wildlife Ecology

UTAH STATE UNIVERSITY
Logan, Utah
2004
ABSTRACT

Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Metapopulation Dynamics, and Population Recovery

by

David C. Stoner, Master of Science
Utah State University, 2004

Presently, eleven western states and two Canadian provinces utilize sport hunting as the primary mechanism for managing cougar (*Puma concolor*) populations. However, the impacts of sustained harvest on population dynamics and demographic structure are not well understood. Additionally, the lack of cost-effective enumeration techniques and strongly conflicting societal values complicate effective management of this species. Given these concerns, the primary goals of this study were (1) to determine the effects of sustained harvest on cougar populations, and (2) estimate the level and extent of cougar harvest statewide.

I monitored cougar populations on Monroe Mountain in south-central Utah, and in the Oquirrh Mountains of north-central Utah from 1999 to 2003. Over this interval the Monroe population was subjected to heavy annual removals and was characterized demographically by a younger age structure, low survival and fecundity, and declining
density. In contrast, the Oquirrh Mountain population was partially protected and exhibited an older age distribution, relatively high survival and fecundity, and static density.

To examine the statewide distribution of sport hunting, I mapped the locations of all cougars legally harvested from 1996-2001, and calculated harvest rates by watershed (# cougars killed / yr / 100 km²). Population trends derived on the study sites under known harvest regimes were used as benchmarks and compared with rates calculated for occupied cougar habitat across the state. This provided an index of where cougar populations were stable or declining as a result of hunting pressure.

Results from this research suggest heavy, sustained harvest can have significant impacts on cougar population dynamics and demographics. Patterns of recruitment resemble a source-sink population structure due in part to spatially variable management strategies. Moreover, these results indicate during the later 1990s, most of the statewide population was exploited at levels equal to or surpassing those measured on Monroe Mountain. Because cougar density and habitat characteristics vary across management units, the temporal scale of population recovery will most likely depend on the interaction of harvest regime, productivity of unexploited populations, and landscape connectivity.
ACKNOWLEDGMENTS

This thesis represents the cumulative input and advice from a large and diverse group of people, without whom I could not have made it this far. The following individuals and organizations were highly influential in the development and completion of this project and are therefore acknowledged here.

A great debt of gratitude goes to my advisor, Mike Wolfe. Mike invited me to work with mountain lions in Utah despite the California baggage - thanks for the pirate’s smile, the holy water, and the hangman’s noose. Many thanks to my committee, Doug Ramsey and Tom DeLiberto who gave freely of their time and provided me with expertise on subjects from aspen-cottonwood competitive interactions to feline physiology.

Many thanks to my predecessor and colleague, David Choate, for helpful advice, insights, and giving me > 3.2% of anything he brought to the table. I am especially indebted to my sponsors and collaborators. The Utah Division of Wildlife Resources provided the lion’s share of the funding and equipment for the study - for their role in facilitating this project many thanks are due to Craig McLaughlin, Alan Clark, and Bill Bates. For providing access to their property, as well as logistical and financial support, thanks go to Douglas Johnson, Lt. Col. Robert Dunton, and Dr. John Crane from the Utah Army National Guard at Camp Williams. To the folks from Kennecott Utah Copper: Dr. Bill Adams, Ann Neville, and Marcelle Shoop - many thanks for support and access to the Shining Mountain; the real treasure is right in front of your eyes. For the warm welcome to Utah, cabin space, and the prettiest mountain in the West, thanks go to Kreig Rasmussen of the Fishlake National Forest.
The effort undertaken to conduct a project of this scope is enormous. Accordingly, sincere appreciation goes to my field crew in all of its various incarnations. To the men from God’s Country, Clint and McLain Mecham. I learned more about mountain lions from the back of a horse than I ever did in the library. If there is a heaven, then it must look like the high country in winter with a fresh track leading the way. For the off-the-record flying lessons, good humor, and eagles-eye perspective, thanks go to Clair Shaffer, Steve Biggs, and Craig Hunt. Thanks also to Byron Bateman, Carey Hendrix (for the hand when I needed it most), Tony Kogianes, Dale McQuillan, Kim Christenson, Greg Jacobson, Amy Seglund, and Meredith Stoner (for the good luck); and to John Paine for Brownie – he was a damn good horse.

Within the university there were a host of people who in their own way kept me on the straight and narrow. I had the distinct pleasure of collaborating on many levels with Debra Carlson, Sandra Cavalcanti, and Nicki Frey. I hope you will recognize our muses within these pages. For GIS and statistical wizardry many thanks are due to Wendy Rieth, Susan Durham, Paul Box, Pat Terletzky, Rob Johnson, Ann Kitchen, Tom Edwards and Kevin Bunnell. Thanks to Esther Beissinger and Cecelia Melder for keeping the books straight. For data, insights, and keen eyes, thanks to Tom Becker, Arlo Wing, and Anita Candelaria, from the UDWR. Thanks to the Millville Predator Ecology Center for use of facilities. Special thanks to Joe Sexton and Mike Ebinger for the insight – the grass really is greener on this side of the fence! Many thanks to Peter Gaede for the illustration. For inspiration, advice, good recommendations, and first-shots, many thanks to friends and mentors, Becky Pierce, Vernon Bleich, Paul Beier, Mike Nelson, David
Mech, and Lee Aulman. To LL for ... everything; and to M.A.D.S. for love, support, and patience ... .

Lastly, thanks for the grudging cooperation, endless games of cat & mouse, and sleepless nights, provided by the Old Hag, the Little Tom, the Big Tom, Ol' #12, 7/11, the Ketamine Queen, Trapfoot, Ol' 58 (the Queen of Kennecott), the Greenwich Bitch (the Phantom of Monroe), and the rest of the gang; its been a long, hard ride.

All my best -

David C. Stoner
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INTRODUCTION

Across western North America sport harvest is the primary mechanism for the population-scale management of *Puma concolor* (Lindzey 1987). Management regimes vary from public safety and depredation-control only in California, to a year-round open season in Texas (Robinson 2000). In order to balance hunting opportunities with protection of big game and livestock, most states manage cougar populations at some intermediate level. However, cougars are secretive, long-lived, and utilize home ranges that exceed those of virtually every other terrestrial mammal in the Western Hemisphere (Gittleman and Harvey 1982), making them difficult to manage with precision (Ross et al. 1996, Logan and Sweanor 2000). At present, there are no widely accepted methods for the enumeration of cougars across diverse habitat types and climatic regimes (Anderson et al. 1992, Ross et al. 1996). Most techniques (track counts, scent stations, probability sampling) have limitations that render them marginally useful (Choate et al. 2003) or capable of detecting only large and rapid changes in population size (Van Sickle and Lindzey 1992, Beier and Cunningham 1996). Additionally, due to their high trophic level, cougars occur at low population densities making them sensitive to perturbations such as prey declines (Pierce et al. 2000, Logan and Sweanor 2001) and over-exploitation (Murphy 1998). Complicating this, populations are subjected to annual removals of varying intensity, but sex and age composition are generally indexed through harvest data, and are therefore subject to non-random sampling biases.

Cougar habitat in Utah is geographically fragmented, being associated with mesic regions between 1,500-3,000 m. The state comprises 4 distinct ecoregions (modified
from Bailey 1980) in which the Wasatch Mountains and associated high plateaus form the core habitat longitudinally bisecting the state. The Colorado Plateau and Great Basin ecoregions consist primarily of desert biomes, with suitable cougar habitat sparsely distributed among insular mountain ranges (Figure 1).

Management is spatially organized, with ecoregions subdivided into 30 different hunting units. Within units, harvest levels are set according to cougar densities modeled from available prey biomass, and select demographic criteria indexed from the prior years harvest (UDWR 1999). Each unit is managed independently in order to apply harvest pressure according to local priorities, which may include intentional density reductions to benefit mule deer (Odocoileus hemionus) or bighorn sheep (Ovis canadensis) populations. Cougars are thus managed at 2 spatial scales. At the local level, they are managed either conservatively as a trophy species, or liberally as a limiting factor in the population dynamics of native ungulates; whereas the statewide population is managed for sustainable hunting opportunities and persistence across its currently occupied range (UDWR 1999).

Unfortunately, little is known about both the immediate and long term effects of sustained harvest on cougar populations (Anderson 1983, Ross et al. 1996). Numerous studies have been conducted on hunted populations (Currier et al. 1977, Ashman et al. 1983, Murphy 1983, Barnhurst 1986, Ross and Jalkotzy 1992, Cunningham et al. 1995), including two removal experiments (Lindsey et al. 1992, Logan and Sweanor 2001). However, few of these studies directly addressed the questions of: (1) how harvest affects the demographic structure of a population, and (2) what the long-term implications are
for persistence and/or recovery of exploited populations. Additionally, habitat configuration and connectivity are important factors influencing cougar recruitment dynamics, however this relationship has been largely overlooked, with the notable exceptions of Beier (1993, 1995), and Maehr et al. (2002). In conjunction with these uncertainties, a growing and increasingly vocal segment of the public concerned with the ecological and aesthetic value of cougars, is demanding greater emphasis be placed on long-term conservation strategies (Robinson 2000, Teel et al. 2002).

Recent years have seen the emergence of the idea of managing cougars on a metapopulation scale based on the effects of natural habitat patchiness (Sweanor et al. 2000, Laundré and Clark 2003) or anthropogenic fragmentation (Beier 1996, Ernest et al. 2003). In general, metapopulations transcend both management unit and state boundaries, necessitating the evaluation of how harvest impacts a local deme, and how patterns of harvest interact with recruitment to shape the overall dynamics of the cougar population. Therefore, understanding the impacts of harvest and subsequent population response is vital in order to manage for persistence across heterogeneous habitats that are being further fragmented by human endeavors.
Figure 1. Cougar habitat (in green) by ecoregion (modified from Bailey 1980) and Management unit-study site locations.
LITERATURE REVIEW

Over the past 3 decades several investigators have argued for the initiation of research comparing exploited and unexploited cougar populations (Hornocker 1972, 1976; Shaw 1981), and for the development of robust enumeration techniques (Anderson 1983).

Regarding hunting, Anderson (1983: 69) remarked "... removal of mature resident pumas...by sport hunting may have a significant effect on the dynamics of puma populations. However, the effects of sport hunting on puma populations have not been evaluated." Lindzey (1991) summarized the most crucial needs for cougar research and management. Two of the top 4 priorities identified were: (1) the development of reliable, cost-effective census techniques, and (2) assessing the impacts of sport harvest on cougar population dynamics and composition. Recommendations generated from Logan and Swenanor’s (2001) monumental New Mexico study included the need for research directed at the effects of human off-take on cougar population dynamics. Concomitantly, the lack of reliable census techniques has been identified by many investigators as the primary impediment to effective management and the prevention of accidental over-exploitation (Anderson 1983, Van Dyke et al. 1986, Quigley and Hornocker 1991, Anderson et al. 1992, Ross et al. 1996, Riley 1998, Logan and Swenanor 2001).

Management Concerns

During the 1990s, a marked increase in the public consumption of an unquantified resource led the Utah Division of Wildlife Resources (UDWR) to commission a study to develop cougar enumeration techniques for broad scale application (Wolfe and Belovsky
In 1999 following a directive from the Utah Wildlife Board, the UDWR convened a committee comprised of scientists and representatives from special interest groups to examine cougar management issues. These issues included: effects of harvest strategies on cougar population and social structure; the need to protect breeding females from over-exploitation; and managing at metapopulation scales. Greater use of GIS applications and the need for increased cooperation and coordination among neighboring states were other matters of concern (UDWR 1999).

These points were formalized in a list of Goals and Objectives, to be implemented through the year 2009. The overarching goal was “to maintain a healthy cougar population within existing occupied habitat while considering human safety, economics, and other wildlife species” (UDWR 1999: 43). Population health was defined as the maintenance of a reasonable proportion of older aged animals; presence of breeding females; lack of disease; balance with prey populations; and evidence of genetic diversity (UDWR 1999: 43). “Reasonable” is interpreted here to mean the preservation of a population structure capable of replacing its losses. Specific objectives outlined in the Cougar Management Plan were: (1) to maintain a healthy cougar population over its current distribution, and (2) to minimize the loss in quality and quantity of existing critical and high priority cougar habitat. Performance targets were established to measure progress in meeting these objectives. Several strategies were identified to achieve these objectives, including the following:

1) Develop harvest regulations that maintain a reasonable proportion of older age animals and breeding females;
2) Implement research findings on population monitoring to determine trend, composition, and relative abundance on a management unit basis;

3) Determine the definition of refuge and evaluate the utility of establishing refugia in the state;

4) Develop a GIS database of the state identifying and measuring cougar habitat, de facto refugia, and critical linkage zones;

5) Work with land management agencies to protect migration/travel corridors in order to maintain genetic diversity within the statewide metapopulation.

This thesis addressed some of the aforementioned management concerns and deficiencies using two approaches. First, I used radiotelemetry to assess the effects of sport hunting on cougar populations by comparing the characteristics of 2 populations managed under notably different levels of exploitation. Second, I used harvest data collected from 1996-2001 to calculate harvest rates for all watersheds ≥ 100 km² within suitable cougar habitat across the state, thereby identifying regions exhibiting harvest rates comparable with those measured on the study populations. Specifically, this study examined the impacts, levels, and distribution of cougar harvest in Utah. I conclude with an alternative framework for managing cougar populations in the absence of reliable census data. The following is a brief review of the concepts employed and the studies conducted, relevant to the questions addressed in this study.
Effects of Hunting on Cougar Populations

The impacts of exploitation on various mammalian species have been reviewed by Reynolds and Tapper (1996), Greene et al. (1998), Frank and Woodroffe (2001), Johnson et al. (2001), and Purvis (2001). Species-specific accounts have been described for several carnivores, including coyotes (Canis latrans; Knowlton 1972), African lions (Panthera leo; Smuts 1978, Creel and Creel 1997), Canada lynx (Lynx canadensis; Bailey et al. 1986), bobcats (Lynx rufus; Knick 1990), polar bears (Ursus maritimus; Derocher et al. 1997), and brown bears (Ursus arctos; Wielgus and Bunnell 2000).

Although many studies have been conducted on exploited cougar populations, few were designed to investigate the role of intense sustained exploitation by humans on population structure. Currier et al. (1977) examined the characteristics of a hunted cougar population on Colorado’s Front Range and concluded that cougar density was sufficient to support the harvest regime in place at that time. Ashman et al. (1983) studied population dynamics in several hunted cougar demes in Nevada. These investigators measured a 30% recruitment rate and recommended harvest not exceed 25% in order to allow the population to compensate its hunting related losses. Murphy (1983) studied an exploited population in Montana and found that recruitment appeared to compensate annual removal rates up to 32% without notable declines in density. Logan et al. (1986a) examined recruitment dynamics of a hunted population in Wyoming and determined that under varying harvest levels, resident removals were compensated by immigration. Murphy (1983) and Logan et al. (1986a) emphasized the role of transient ingress from neighboring unhunted watersheds in maintaining densities of exploited populations.
Cunningham et al. (1995) studied a cougar population in southern Arizona subjected to heavy depredation control measures. Removal of resident animals in this population was correlated with some of the lowest survival values measured for the species, yet density remained stationary. These investigators also noted that male immigrants were predominantly mature animals. Ross and Jalkotzy examined the characteristics of an exploited cougar population in southern Alberta and found, similar to Logan et al. (1986a), the population seemed capable of “rapidly replacing its losses” following a reduction in hunting pressure (1992: 424). In Wyoming, Anderson (2003) assessed the response of a population to manipulation by examining sex and age trends by means of harvest data. He then compared these figures to a pseudo-control (lightly exploited) population. Anderson speculated that social disruption was minimized by resting the unit from hunting pressure for 2-3 years following reductions.

It is important to note that none of these investigations were specifically designed to assess the impacts of harvest on the demographic structure of the study population, but the conclusions drawn were an artifact of site selection and policy decisions at the time the studies were initiated.

**Metapopulation Dynamics**

Population growth is achieved via two parameters: resident reproduction and immigration (Donovan and Strong 2003). The relative contribution of these parameters may be influenced by the configuration of habitat. Cougars require habitats that are often patchily distributed in space. Individuals are aggregated in areas of suitable habitat
separated by varying amounts of sub-optimal habitat, in some cases contributing to the formation of discrete demes (McCullough 1996, Ritchie 1997). These demes may be connected in varying degrees by subadult dispersal (Beier 1995, Sweanor et al. 2000) or seasonal migrations (Pierce et al. 1999). The former behavior may contribute numerically to the recipient deme if habitat connectivity is high, or genetically through the occasional infusion of new alleles (Loxterman 2001, Sinclair et al. 2001, Ernest et al. 2003). Because the distribution of suitable cougar habitat in Utah is spatially subdivided the species’ distribution may be viewed as a metapopulation (Levins 1969, Harrison 1994, McCullough 1996). That is, it comprises a collection of sub-populations with varying degrees of interaction, and potentially uncorrelated dynamics. The basic tenets of metapopulation theory are: (1) populations are spatially structured into assemblages of local breeding populations, (2) emigration and immigration among sub-populations has some effect on local dynamics, and (3) this effect includes the possibility of occasional extinction / recolonization events (Levins 1969, Hanski and Simberloff 1997). Hanski and Simberloff argued that the latter characteristic is the mark of a “true” metapopulation. McCullough (1996), prompted by the need for an operational definition suitable for management purposes, proposed 2 salient features for metapopulations as: (1) a spatially discrete distribution, and (2) a non-trivial probability of extinction in a least one or more local patches. Harrison (1994) argued that a spatially structured population does not necessarily constitute a metapopulation if dispersal among demes is either too frequent (panmictic population), or never occurs at all (non-equilibrium metapopulation). However, for conservation purposes she proposed an even simpler definition for
metapopulation as “any set of conspecific populations, possibly but not necessarily interconnected” (Harrison 1994: 111). Further discussion of metapopulations will refer to this more liberal definition.

No cougar study has yet been, nor is likely to be, conducted over a sufficient temporal or spatial extent to observe the kind of environmental perturbations (e.g. droughts, prey declines, and climate change) or stochastic events (disease epidemics) it would require to measure extinction and recolonization episodes (Doak and Mills 1994). Nevertheless, the metapopulation model has been invoked in reference to cougar populations in California, New Mexico, and the Great Basin (Beier 1996, Sweanor et al. 2000, Ernest et al. 2003, Laundre and Clark, 2003), as well as fragmented felid populations elsewhere (Jackson and Fox 1995, Smith et al. 1999, Ferreras 2001). In the absence of robust enumeration techniques, the construct shows promise as a framework for the management of highly mobile and low-density species.

**Source–Sink Dynamics**

Whereas the metapopulation concept emphasizes the size and distance among habitat patches across a landscape, the source-sink concept focuses on the density-dependent processes occurring within demes. This model assumes that habitat quality varies among patches. Populations in the most productive patches (sources) exist at saturation levels and reproduction exceeds the ability of the habitat to absorb internal recruitment (Pulliam 1988). Surplus individuals either become floaters (transients) in the natal deme, or emigrate to areas of lower habitat quality, termed sinks. A sink population is one in
which habitat quality is poor, and consequently mortality exceeds reproduction. The sink population achieves the majority of its recruitment from immigration and it is assumed that the population could not sustain itself without this contribution. Due to the lack of immediate breeding opportunities in the natal deme, the fitness of recruits in the source is assumed to be greater if they disperse. Sink habitats typically have lower population density and provide relatively more breeding opportunities than if the individual lived as a non-breeding floater in the source population. Ritchie (1997) argued that the metapopulation and source-sink concepts are not mutually exclusive, and that source-sink populations and metapopulations can grade into one another depending on the degree of demographic connectivity. More succinctly, each model focuses on different parameters as drivers of population dynamics. Due to the inability to measure extinction / recolonization events for long-lived and widely distributed species (Harrison 1994), the source-sink model may be a better way of examining differential, habitat-based population dynamics within the context of a large spatially structured (meta) population.

Management Regime as a Component of Habitat Quality

In heavily exploited populations in situ reproduction may not keep pace with mortality, making the immigration component of population growth particularly important. Pulliam’s (1988) model hinges upon habitat quality and density-dependent breeding opportunities as the overriding factors determining whether a deme exhibits source or sink characteristics. Here however, I was interested not necessarily in the environmental quality of the habitat patch, but in management regime as a factor
imposing positive or negative characteristics on a given patch. Two patches may possess the same environmental qualities (food resources, security, etc.) but the population in one may display lower survival due to human influence, i.e. hunting pressure. Therefore my arguments regarding source-sink population dynamics refer to the whole character of the site, incorporating the nature of prevalent interactions with humans. Other investigators also have used the source-sink model in reference to management related influences (Van Vuren and Smallwood 1996, Woodruffe and Ginsburg 1998). Several investigators have invoked or implied this general immigration driven phenomenon in cougars (Murphy 1983, Logan et al. 1986a, Cunningham et al. 2000, Logan and Sweanor 2001), and other wide ranging, exploited, or patchily distributed carnivores (Bailey et al. 1986, Knick 1990, Litvaitis et al. 1996, Noss et al. 1996, Delibes et al. 2001, Ferreras 2001, Johnson et al. 2001, Mauritzen et al. 2002).

**Population Recovery**

The most notable examples of studies examining the effects of harvest on cougar populations were the experimental removals conducted in Utah and New Mexico by Lindzey et al. (1992), and Logan and Sweanor (2001), respectively. These studies measured recovery rates and assessed population resiliency following declines commensurate with typical harvests. Lindzey et al. (1992) found that a removal of 27% of the harvestable portion of the population was not replaced by the beginning of the following hunting season, 9 months post-removal. Their results were confounded by non-human mortalities that took place during the recovery phase, suggesting that harvest
may be additive to other sources of mortality. Building upon these results, Laing and Lindzey (1993) studied patterns of resident replacement and found that recruitment of females was primarily achieved via philopatric behavior of resident progeny, while immigration accounted for male recruitment. Logan and Sweanor (2001) performed a similar experiment in New Mexico, in which 58% of the adult/subadult population was removed. This protected population required > 31 months to recover to its former level by means of the same recruitment mechanisms noted by Laing and Lindzey (1993).

Anderson (2003) documented similar results in a Wyoming population. In all of these cases, the treatment represented one-time reductions of a single population. To date, no study has been conducted simultaneously on two populations in which one was subjected to sustained (>5 years) harvest while the other was left unmanipulated.

Aside from reproduction and immigration, factors facilitating population recovery following density reductions have not been examined adequately. Landscape connectivity has been identified as a significant factor preventing dispersal and gene flow among populations of tigers (*Panthera tigris*; Smith 1993), Florida panthers (*P. c. coryi*; Maehr 1997), Iberian lynx (*Lynx pardinus*; Ferreras 2001), and for a suite of other carnivores (Sunquist and Sunquist 2001). Beier (1993, 1995, 1996) provided a notable example of the influence of landscape connectivity in his study of movement corridors connecting sub-populations of cougars in a severely degraded urbanized Southern California environment. Beier (1993, 1995) found that narrow, linear habitat segments served as dispersal conduits for transients moving between demes, and for resident males moving between disjunct female home ranges. These corridors became the focus of land
conservation efforts due to their disproportionately large influence on population persistence. Other investigators have qualitatively noted the importance of landscape connectivity in the facilitation of demographic connectivity between regions of high and low exploitation (Lindzey et al. 1989, Anderson 2003).

**Surrogates for Identifying Source and Sink Populations**

Because habitat quality varies and accurate prey density estimates may not be available, surrogates are needed to assess whether an area tends toward source or sink-type dynamics. Exploitation levels may offer one such index. If critical harvest rates at which population densities decline exist, then the distribution of this rate may offer insights as to where populations are being harvested at sustainable or unsustainable levels. Ideally, critical rates could be measured for cougar populations existing over a range of densities and environmental conditions.

Protected areas may act as source populations. Lindzey (1987: 666) noted, “parks and large remote areas where hunting is either prohibited or restricted by lack of access may act as refuges.” Murphy speculated that his Montana study population was subsidized by immigrants from unhunted drainages in the Idaho roadless area, which acted as a *de facto* refuge and consequently functioned as a source population. Powell et al. (1996) and Beringer et al. (1998) found higher survival among black bears residing in a North Carolina sanctuary. Based on harvest returns of bears dispersing from the refuge, these authors suggested the unhunted area was functioning as a source population. Consistent reproduction and dispersal from protected areas have been noted as the principal factors
in sustainable harvests of numerous game species, including Canada lynx (Bailey et al. 1986), bobcats (Knick 1990), fox squirrels (Sciurus niger; Herkert et al. 1991), black bears (Schwartz and Franzmann 1992), and moose (Alces alces; LaBonté et al. 1998). This phenomenon appears to be a function of resource availability, breeding opportunities, and dispersal patterns. Based on these examples, the spatial distribution of protected populations and those vulnerable to overexploitation may be surrogates for identifying source and sink populations or population segments.

**Alternative Management Strategies for Cougars**

Protected areas have been a formal component wildlife management in North America at least since the establishment of Yellowstone National Park in 1872 (Wolfe et al. 2002), and in Europe at least since the 17th century (Leopold 1933). Aldo Leopold, in his classic treatise, *Game Management* (1933: 195) stated, “A game refuge is an area closed to hunting in order that its excess population may flow out and restock surrounding areas.” He further, noted that “outflow” [emigration] was the fundamental mechanism defining a functional refuge. Although not identified as such, this definition corresponds to a management-based source and sink system. More recently, McCullough (1996) developed this idea further, and suggested for populations lacking detailed census data, a mosaic of hunted and unhunted regions may provide high yields while minimizing the risk of overexploitation. Noss et al. (1996) emphasized the role of refugia in reserve design for wide-ranging carnivores due to the spatial requirements of a viable population. Influenced by McCullough (1996), Riley (1998: 117) stated, “Spatially structured harvest
systems 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." Logan and Sweanor (2001) developed a succinct management strategy specifically for cougars based on the concepts noted above, which they dubbed Zone Management. The idea featured a system of designated refugia surrounded by areas subject to varying degrees of harvest. This system was designed for a statewide perspective, where harvest levels are set as a function of the severity of local conflicts with cougars, but supported by two ≥ 2,400 km² inviolable sanctuaries, which act to stabilize the metapopulation. This represents the first such attempt to manage cougars using a system of formal refugia. In the absence of standardized and statistically sound enumeration methodology, a spatial approach incorporating metapopulation theory and known sustainable harvest rates is likely to be the best viable alternative for managing statewide cougar harvest, thus insuring both ample hunting opportunities and long-term persistence of the metapopulation.
RESEARCH OBJECTIVES

This study was designed to accomplish 2 overarching goals, namely: (1) to assess the impacts of exploitation on cougar population characteristics, and (2) develop an index for evaluating harvest levels statewide. The Monroe and Oquirrh Mountain Cougar Management Units were the primary study sites for examining these questions (Figure 1). Although differences exist between the study sites in terms of size, vegetation composition, and prey species ratios, they are climatically similar and located within 190 km of each other, making them ecologically similar in a broad sense, but far enough apart to be treated demographically as independent populations. The most profound difference between these populations is the management regime to which each is subjected.

The specific objectives of this study were:

1) To assess how harvest levels might influence the demographic structure of individual populations;

2) To assess how the distribution of these impacts might affect recruitment within the cougar metapopulation;

3) Identify the factors that influence the rate of population recovery;

4) Map the distribution of harvest and assess exploitation levels relative to study site means and population trends.

Based on these objectives I developed 3 hypotheses: (1) heavy exploitation would increase the rate of resident turnover, thus creating habitat vacancies that would be filled by a combination of resident progeny and immigrants (Laing and Lindzey 1993, Logan
and Sweanor 2001), (2) different levels of exploitation would create localized population sinks influencing regional metapopulation dynamics (Cunningham et al. 2000, Delibes et al. 2001), and (3) the rate of population recovery would be influenced by resident fecundity, proximity to minimally exploited demes (Murphy 1983, Lindzey et al. 1992), and landscape connectivity (Beier 1993).
STUDY AREAS

Exploited Area

Monroe Mountain comprises part of the Sevier Plateau in the Southern Mountains ecoregion in south-central Utah (~38.5° N, 112° W; Figure 2). The mountain is a high volcanic plateau extending 75 km in a north-south orientation, and lies along a west to east geologic transition from basin and range topography to the Colorado Plateau. Monroe’s streams drain into the Great Basin, however climatically and biologically it is more closely associated with other high elevation regions in the Colorado Plateau and southern Rocky Mountains. The Southern Mountains ecoregion exhibits what are thought to be the highest cougar densities in the state, with consequently higher harvest rates than any other ecoregion in Utah (UDWR unpublished data).

The study site covers ~1,300 km², and encompasses the central unit of the Fishlake National Forest, southeast of Richfield, Utah, in Sevier and Piute counties. Other landholders include the Bureau of Land Management (BLM), State of Utah, and various private interests. The terrain is rugged, ascending from broad sagebrush flats at 1,600 m to sub-alpine forests and meadows at 3,400 m. Steep canyons dissect the range and provide access points for roads and trails to the ridges, peaks, and mid (~2,700 m) elevation plateaus (Wolfe et al. unpublished).

Annual precipitation ranges from 15-20 cm in the Sevier Valley, to 60-120 cm on the plateaus above 2,700 m. Precipitation falls primarily as snow in January and February, with ~40% falling as summer rain (Ashcroft et al. 1992). Average monthly temperatures
range from \(-4^\circ C\) in January to \(20.7^\circ C\) in August. Snowpack typically persists until mid-June at elevations > 3,000 m. Temperature discrepancies of \(10^\circ C\) often exist between the valley floor and the upper plateaus.

Monroe Mountain supports 19 vegetative types (Edwards et al. 1995), with the largest (44%) area dominated by piñon-juniper woodlands \((Pinus edulis, Juniperus scopulorum, J. osteosperma)\). Mixed conifer \((Picea engelmannii, P. pungens, Abies lasiocarpa, Pseudotsuga menziesii)\) and aspen \((Populus tremuloides)\) stands occur at higher elevations, with gambel oak \((Quercus gambelii)\), mountain shrub (e.g., Cercocarpus ledifolia, Rosa woodsii) patches and mixed sagebrush \((Artemesia tridentata)\) - grassland meadows interspersed throughout (Wolfe et al. unpublished).

Resource exploitation includes livestock grazing, logging, and recreation (primarily use of all terrain vehicles and hunting). The UDWR classifies Monroe Mountain as Cougar Management Unit no. 23. Mule deer and elk \((Cervus elaphus)\), the primary cougar prey species on this site, are also managed for annual harvests. Human densities around the site vary from \(73 / 100 \text{ km}^2\) in Piute County to \(382 / 100 \text{ km}^2\) in Sevier County (www.governor.utah.gov/dea/demographics/demdata.htm), with most of the population scattered in small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.
Monroe Mountain Study Site

Figure 2. Monroe Mountain study site in south-central Utah (Unit 23). Green indicates suitable cougar habitat; white represents alpine and subalpine biomes.
Protected Area

The Oquirrh-Traverse Mountains complex (hereafter ‘the Oquirrhs’), is dominated by limestone and granite, and extends 55 km in a north-south orientation on the eastern edge of the Basin and Range ecoregion (Chronic 1990; Figure 3). The center of the study area is located near 40.5° N, 112.2° W in north-central Utah. The Oquirrhs are typical of other ranges within the Basin and Range Province in that they represent islands of high productivity relative to the surrounding desert basins (Brown 1971). These isolated ranges represent the majority of cougar habitat in this ecoregion.

The total area of the Oquirrhs measures ~ 950 km², but fieldwork was conducted primarily on the northeastern slope of the range, on properties owned and managed by the Utah Army National Guard (Camp W. G. Williams, Traverse Mountains, 100 km²) and the Kennecott Utah Copper Corporation (Oquirrh Mountains, 380 km²). The site is situated at the southern end of the Great Salt Lake, abutting the southwestern side of the greater Salt Lake metro area, and straddles the Salt Lake, Utah, and Tooele county boundaries. Ownership on the southern and western portions of the Oquirrhs is a conglomeration of BLM, cattlemen’s associations, and small mining interests. Approximately 45% of the range is in private ownership.

Elevations on the site vary from lake level at 1,280 m up to 3,200 m. The Traverse Mountains run perpendicular to the Oquirrhs and vary in elevation from 1,650 m to 2,100 m. The east side of the Oquirrhs has deep soils and extensive gently rolling foothill regions interspersed with shallow canyons and draws. In contrast, the west side is
characterized by rugged canyons, abrupt elevational gradients, and a much higher degree of exposed bedrock.

Annual precipitation ranges from 30-40 cm in the Salt Lake and Tooele valleys to 100-130 cm on the highest ridges and peaks. Most precipitation falls as snow between December and April, with approximately 25% coming in the form of summer thunderstorms. Average monthly temperatures range from –2.4°C in January to 22.2°C in July (Ashcroft et al. 1992).

Major vegetation types include sagebrush interspersed with gambel oak and Utah juniper in the low to mid elevations; mountain mahogany (Cercocarpus spp.) predominates on dry rocky ridges, and big-toothed maple (Acer grandidentatum) in the drainages at low elevations and across broader areas above 1,800 m. North facing slopes above 2,200 m comprise subalpine communities of aspen and Douglas fir, whereas limber pine (Pinus flexilis) inhabits the crest of the range (Edwards et al. 1995).

Resource exploitation and industrial activities are intensive, and have been dominated by mining and military training for > 100 years (Roylance 1982). Kennecott’s facilities include 2 large open pit mines and attendant infrastructure. Camp Williams is used primarily as an artillery and small arms range, and consequently exhibits brief fire return intervals. In addition, all prominent peaks on the study site support commercial radio and television transmitters with associated access roads. A limited amount of livestock grazing occurs seasonally (CW - cattle and sheep; Kennecott - cattle and horses). The study site is part of the Oquirrh-Stansbury Cougar Management Unit no. 18, but both of these properties are closed to the public, and cougar hunting is prohibited. Human
density in the region is highly variable, with rural Tooele County having 232 / 100 km², while urban Utah County has 7,181 / 100 km² and Salt Lake County exhibits the highest human density in the state with 47,259 / 100 km² (www.governor.utah.gov/dea/demographics/demdata.htm).
Figure 3. Oquirrh-Traverse Mountain study site in north-central Utah (approximately 25% of total cougar habitat within Unit 18). Green indicates suitable cougar habitat; white represents alpine and subalpine biomes.
METHODS

Cougar populations within the 2 study areas were monitored simultaneously from early 1997 to the summer of 2003. Demographic parameters were estimated for each population based on radiotelemetry data collected between 1996-2003 on Monroe, and from 1997-2003 on the Oquirrhs. All descriptive statistics are reported as mean ± SE unless otherwise noted. Statistical comparisons were performed using either SAS (V.8) or Minitab (V.13) software.

Radiotelemetry and Harvest

Intensive capture efforts were conducted during winter (November to April) each year of the study. Cougars were captured by pursuing them into trees, culverts, cliffs, or mineshafts using trained hounds (Hemker et al. 1986) and then immobilized with a 5:1 combination of ketamine HCl and xylazine HCl (Logan et al. 1986b) at a dose of 10 mg ketamine plus 2 mg xylazine/kg body weight. Immobilizing drugs were administered with a Palmer CO₂ pistol (Powder Springs, GA), jab-stick, or hand-held syringe. A vestigial premolar (P2) was removed for age determination by counts of cementum annulations, and a blood sample was taken for genetic analyses. Cougars were sexed, aged, weighed, measured, tattooed with a unique identifier, and equipped with a radio-collar (Advanced Telemetry Solutions, Isanti, MN) and a micro-chip (AVID Co., Norco, CA). Adult females were checked for evidence of lactation during handling. Kittens too small to wear a radio-collar were tattooed and released. All procedures were conducted
in accordance with Utah State University Institutional Animal Care and Use Committee (IACUC), approval no. 937-R.

Radio-collared cougars were subsequently relocated using aerial and ground-based telemetry to plot radio-triangulated locations on USGS 7.5' topographic quads using Universal Transverse Mercator (UTM) coordinates (Zone 12, NAD 27), which were entered into a GIS database (ArcView, ESRI Products, Redlands, CA). Aerial telemetry flights were conducted bi-monthly on both sites when weather conditions permitted.

Over the course the study, the Monroe Mountain Cougar Management Unit was open to cougar hunting, and radio-collared individuals were not protected from harvest beyond the normal legal stipulations outlined in the UDWR hunting proclamations. Annual hunter-kill was regulated by apportionment of a limited number of hunter permits, issued by the UDWR on the decision of the State Wildlife Board (Wolfe et al. unpublished).

The Camp Williams and Kennecott properties were closed to hunting throughout the study; however, cougars leaving those properties were subject to harvest during the hunting season on adjacent private and public lands within Unit 18.

**Demographic Parameters**

*Age Structure.*—Age was determined at the time of capture using visual inspection of tooth wear and gumline recession (Ashman et al. 1983, Laun dré et al. 2000). Cementum annulations (Trainer and Matson 1988) were used for aging animals for which no other estimates were available. Tooth samples were not collected for all animals marked, and some were broken during extraction, therefore I relied primarily on visual inspection and
gumline recession for age determination. I initially classified each animal as an adult (>2.5 yrs), subadult (1.5-2.5 yrs), or as a kitten (<1.5 yrs). I compared differences in mean ages within sexes / between sites, and for all cougars between sites using ANOVA and Tukey’s pairwise comparisons. All data were tested for normality, and log transformed where needed in order to meet statistic assumptions.

Cause-Specific Mortality.—Causes of cougar mortality were determined through visual inspection and necropsy of carcasses. When cause of death could not be determined in the field, the carcass was submitted to the USU Veterinary Diagnostics Lab for detailed analysis. Mortality was calculated by tallying cause of death among radio-collared animals, and in a few instances, unmarked animals found opportunistically during tracking sequences. Mortality causes were pooled as “human” and “non-human,” and tested for proportional differences using chi-square ($\chi^2$) tests.

Survival.—Survival was calculated annually for all monitored adult and subadult animals from each population. To account for censoring due to the duration of additions and losses of radio-collared individuals to the sample, I used a Kaplan-Meier product limit estimator (Kaplan and Meier 1958). Annual survival was estimated by defining the start of sample intervals as 1 December of each year. This ensured that human-related mortality is accounted for only once during a single non-overlapping period in each year, by sampling prior to the beginning of the hunting season (Wolfe et al. unpublished). Annual survivorship was calculated as the product of the survival for all measured intervals, j,
\[ S(t) = \prod \left[ \frac{r(T_j) - d(T_j)}{r(T_j)} \right] \]

where \( r(T_j) \) is the number of cougars alive at the beginning of a time interval \( T_j \), and \( d(T_j) \) is the number of cougars actually dying within that interval. The variance for each interval was then calculated according to Greenwood’s formula (Cox and Oakes 1984, as cited in White and Garrot 1990) as:

\[
\text{Var}[S(T_j)] = S^2(T_j) \sum \frac{d(T_j)}{r(T_j)[r(T_j) - d(T_j)]}
\]

with the 95% confidence interval \((\alpha = 0.05)\) then:

\[ S(t) \pm 1.96 \ (\text{Var}[S(T_j)])^{1/2} \]

This method provided the most latitude for measuring this parameter in an observational study (Wolfe et al. unpublished).

_Fecundity._ — Fecundity was measured as the proportion of litters-of-the-year detected per adult female on site during winter. Litters were counted during snow tracking and capture efforts. Kittens > 3 months old are only detected with their mothers 20-43% of the time (Barnhurst and Lindzey 1989), however many female cougars were tracked on multiple occasions, increasing the probability of detecting kittens if present. All counts were considered a minimum estimate of the number of litters present. I did not attempt any analyses on the actual number of kittens born / litter due to the difficulty in
determining the actual number of kittens when $\geq 2$ track sets were found. Therefore the number of kittens / litter is biased low. The minimum percentage of females caring for young provided a relative estimate of productivity of each population (Barnhurst and Lindzey 1989). I used t-tests to detect differences in mean fecundity pooled over the entire study interval.

**Density.**—Cougar density was measured as the total number of adult and subadult cougars / 100 km$^2$ present. In this sense, I attempted to conduct a census of the population during winter. The population was estimated by using the sum of 3 different sources of detection. The baseline count consisted of all cougars captured and radio-collared. Second, tracks of animals pursued but not captured, which did not correspond to a radio signal, were assumed to be unmarked animals and were included in the population estimates regardless of residency status. Males and females can generally be differentiated by track size (Fjelline and Mansfield 1989), therefore in order to reduce the potential for double counting, multiple track sets of the same-sexed animal encountered in the same general area were considered 1 individual. Third, uncollared harvested animals that could not be accounted for from tracking sequences in the location of the kill were also included. The population estimate was summed in June after the capture and hunting seasons had ended, and most accurately represented the population during the period December to March.

Road densities were high across both study areas providing sufficient access, but winter tracking efforts were conducted by horseback and snowmachine in addition to road surveys to reduce bias associated with access (or lack there of). This also helped to
reduce bias in terms of the social classes most vulnerable to detection due to frequent road crossings or small home ranges (Barnhurst 1986). Snow conditions are influential in track detection ability and therefore dry winters may have some bias associated with population estimates, however this bias was likely consistent between sites, as both study areas are subject to similar weather patterns.

Study area boundaries were based on major roads surrounding the site, therefore I used ecologically relevant vegetative and topographic features to delineate and quantify habitat within the study site perimeter. I followed the criteria of Laing and Lindzey (1991), which excluded valley bottoms and landcover types dominated by urban and agricultural uses, and shrublands with slopes < 8°. Maps represent geographical area on the planar surface and do not account for slope differences in mountainous terrain where actual surface area is greater. This discrepancy in area calculation leads to an increasing overestimation of population density as the ruggedness of the terrain increases. Therefore to increase the accuracy of the density estimates, GIS software (ArcView surface/area ratio extension, Jenness Enterprises, Flagstaff, AZ) was used to calculate the actual surface areas of habitat within study site perimeters.

Dispersal.—All kittens handled on the Oquirrh mountain site were tattooed in each ear in the event that they were subsequently captured as adults. For the Oquirrh Mountain animals, I was able to calculate several crude estimates of dispersal distance and direction opportunistically based on harvest returns of animals marked as kittens. In addition, subadults captured as transients on Monroe were monitored via radiotelemetry
for extra-site movements, thereby providing some information on coarse-scale movement patterns.

**Landscape Configuration**

Measures of landscape configuration were used to assess the overall degree of connectivity of the study sites to surrounding habitats within their respective ecoregions. Connectivity is defined here as “the degree to which the landscape facilitates or impedes [animal] movement among resource patches” (Taylor et al. 1993: 571). Metrics derived were size (km²), shape (perimeter-area ratios), greatest interpatch distance, percent of perimeter connected to neighboring habitat patches, width of connective habitat, and percent of perimeter impermeable to cougar movement. Impermeability refers to landscape features that prohibited, filtered, or redirected animal movement, such as the Great Salt Lake or Interstate 15 (Noss et al. 1996, Ernest et al. 2003, Forman et al. 2003). Perimeter-area ratios provided a relative measure of how circular, or how much edge one region has relative to another (Turner et al. 2001). These measures were derived in ArcView (spatial analyst extension) using a 30 m digital elevation model (DEM) of the state of Utah.

**Harvest Rates and Distribution**

*Study Site Harvest Rates.*—Harvest rates for each study population were calculated as the sum of all human caused mortality (hunting, poaching, depredation control, and roadkill), for the interval 1996-2001 divided by 6 (number of hunting seasons over the interval), and then adjusted for area. The results were standardized harvest rates
measured as a density (no. cougars killed / yr / 100 km²) for each study area. This number included all animals (marked and unmarked) harvested on the unit, in order to be comparable with other units for which no reliable population estimates existed.

Statewide Harvest Rates.—Accurate cougar population counts and trends were not available for any region of the state outside of the study areas. In order to compare harvest rates calibrated on the study sites, I acquired data from the UDWR for all cougars legally harvested from 1996-2001. Kills were assigned UTM coordinates based on drainage names taken from BLM 1:100,000 scale topographic maps. I then overlaid a 1:500,000 scale watershed coverage from the Utah Automated Geographic Reference Center (AGRC) and lumped all drainage-kill associations into the appropriate watersheds clipped from a model of predicted cougar habitat (Edwards et al. 1995, UDWR 1999). Due to the imprecision of estimated locations, I used ArcView to calculate harvest rate as kill-density-by-watershed, using the same methods noted above. I mapped harvest rates for all watersheds ≥ 100 km² for illustration. However results of this analysis are only discussed for watersheds ≥ 500 km² so that spatial units were roughly comparable to the Oquirrh Mountain study site, representing the minimum spatial extent for which both population trends and harvest regime were well documented. Watersheds were then categorized and mapped according to 3 harvest rates: those ≤ Oquirrh rates; those greater than the Oquirrh but less than Monroe; and those ≥ Monroe. Because study site cougar densities and population trends were known, this method provided a coarse measure of exploitation levels and served as an index to population trends during the sample interval. Thus I was able to identify watersheds exploited at levels that corresponded to known
trends in populations managed under nominal (Oquirrh site), and heavy harvest (Monroe rates). Anything falling between these levels was labeled as “undetermined.”
RESULTS

Radiotelemetry and Harvest

_Capture._—Ninety-one individual cougars were captured and marked between the two study sites, representing 121 capture events (Table 1). Captures were conducted on Monroe from January 1996 to March 2003 and on the Oquirrh site from February 1997 to April 2003. Capture-related mortality consisted of 3 kittens (1♂, Monroe; 2 ♀, Oquirrhs) and 2 adults (1♂, Monroe; 1♀, Oquirrhs). All 3 kittens and the adult female and were killed by tracking hounds; the adult male died of respiratory complications during anesthesia. This constitutes a capture-mortality rate of 4.1%, which is within the 5% allowed by IACUC protocol.

Table 1. Age classes and sexes of cougars captured, Monroe and Oquirrh Mountain study sites, Utah, 1996–2003.

<table>
<thead>
<tr>
<th>Age class / sex</th>
<th>Monroe</th>
<th>Oquirrhs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>Males</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Sub-adults</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>12</td>
<td>2</td>
</tr>
<tr>
<td>Males</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Kittens</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Males</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Totals</td>
<td>49</td>
<td>42</td>
</tr>
</tbody>
</table>
The ruggedness of terrain and frequent animal use of lava tubes, mineshafts, and culverts hindered the collection of ground-based telemetry observations. Consequently most telemetry data were derived from aerial surveys (Table 2). On both sites, females were monitored for 2-4 times longer than males, reflecting the smaller sample of males, greater tendency to emigrate from the study sites, and their shorter residence times. I calculated error radii by ground truthing mortality sites, collars dropped by kittens, or experimentally placed collars (N=20), as the linear distance between the estimated and actual location of the collar. The mean error radius for aerial telemetry points was 645 m (range = 27-3,255 m).

Monroe Mountain Cougar Harvest.—For the period 1990-95, prior to initiation of this study, a mean of 15.6 (range = 14-19) hunting permits were issued annually, corresponding to a mean kill of 8.7 cougars/yr (range = 6-12), and a mean hunter success

Table 2. Summary radio-telemetry data for marked cougars, Monroe and Oquirrh Mountain study sites, Utah, 1996-2003.

<table>
<thead>
<tr>
<th>Site</th>
<th>Sex</th>
<th>n</th>
<th>Mean</th>
<th>SE</th>
<th>Range</th>
<th>n</th>
<th>Mean</th>
<th>SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monroe</td>
<td>Females</td>
<td>764</td>
<td>28.3</td>
<td>0.9</td>
<td>1-85</td>
<td>16,943</td>
<td>627.5</td>
<td>4.2</td>
<td>2-2552</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>148</td>
<td>7.4</td>
<td>0.7</td>
<td>1-23</td>
<td>2,837</td>
<td>141.9</td>
<td>2.7</td>
<td>3-494</td>
</tr>
<tr>
<td>Oquirrh</td>
<td>Females</td>
<td>586</td>
<td>34.5</td>
<td>1.5</td>
<td>4-105</td>
<td>12,753</td>
<td>750.2</td>
<td>7.0</td>
<td>14-2226</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>147</td>
<td>13.4</td>
<td>0.9</td>
<td>1-36</td>
<td>3,930</td>
<td>357.3</td>
<td>5.7</td>
<td>3-1173</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>1,645</td>
<td></td>
<td></td>
<td></td>
<td>36,463</td>
<td></td>
<td></td>
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</tbody>
</table>
of 54.0% (range = 40.7-64.9%; Maxfield 2001). In 1996, the number of permits issued increased 33.7% over the 1990-95 mean. In 1997, the number of permits increased 40% over 1996 levels, and 151% over the 1990-95 mean. Between 1998 and 2000, the number of permits issued decreased to 1990-95 mean levels, and was again decreased for the 2000-01 season. During the years of heavy harvest (1997-2001), mean per-capita hunting pressure was 90.7% (range = 71.4-100%), i.e. the proportion of the population that was legally harvestable. Mean per-capita hunting pressure was 27.2% (range = 25-29.4%; Table 3) during the years of light harvest (2002-2003). Over the course of the study a total of 159 permits were issued, 75 cougars (48 ♂, 27 ♀) were harvested, and total hunter success was 47.1%, while mean annual hunter success was 52.4% (Table 3).

Table 3. Cougar harvest characteristics from Monroe Mountain (Unit 23), 1996-2003 (Maxfield 2001 and UDWR unpublished).

<table>
<thead>
<tr>
<th>Hunting Season</th>
<th>Estimated population</th>
<th>Permits issued</th>
<th>Cougars killed</th>
<th>% Kill female</th>
<th>Percent of population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Huntable¹</td>
</tr>
<tr>
<td>1996</td>
<td>35</td>
<td>24</td>
<td>14</td>
<td>42.9</td>
<td>68.5</td>
</tr>
<tr>
<td>1997</td>
<td>42</td>
<td>40</td>
<td>17</td>
<td>47.1</td>
<td>95.2</td>
</tr>
<tr>
<td>1998</td>
<td>33</td>
<td>30</td>
<td>15</td>
<td>26.7</td>
<td>90.9</td>
</tr>
<tr>
<td>1999</td>
<td>26</td>
<td>25</td>
<td>7</td>
<td>28.6</td>
<td>96.1</td>
</tr>
<tr>
<td>2000</td>
<td>21</td>
<td>15</td>
<td>9</td>
<td>44.4</td>
<td>71.4</td>
</tr>
<tr>
<td>2001</td>
<td>15</td>
<td>15</td>
<td>6</td>
<td>33.3</td>
<td>100.0</td>
</tr>
<tr>
<td>2002</td>
<td>17</td>
<td>5</td>
<td>3</td>
<td>33.3</td>
<td>29.4</td>
</tr>
<tr>
<td>2003</td>
<td>20</td>
<td>5</td>
<td>4</td>
<td>0.0</td>
<td>25.0</td>
</tr>
<tr>
<td>Means ± SE:</td>
<td>26.1 ± 9.6</td>
<td>19.9 ± 12.2</td>
<td>9.4 ± 5.3</td>
<td>32 ± 15</td>
<td>72.1 ± 30.0</td>
</tr>
</tbody>
</table>

¹Per-capita hunting pressure, i.e. the ratio of the number of permits issued to the estimated population size (column 3 / column 2).
Oquirrh Mountain Cougar Harvest.— From 1996 to 2001 radio-collared animals on Unit 18 were considered legally harvestable. Cougars on the National Guard and Kennecott properties were protected, but these properties were surrounded by private and public lands open to hunting making any study animal found off-site legal quarry. Beginning with the 2002 season, all radio-collared animals on the unit were protected by law regardless of property ownership. For Unit 18, a total of 105 permits were issued during the course of the study, averaging 15/yr (range = 11-20). This resulted in a kill of 66 cougars (39 ♂, 27 ♀). Hunter success averaged 61.8% (range = 55-85%), with approximately 50% of harvested cougars removed from the Oquirrh Mountain portion of the unit (Figure 1). During the course of the study 5 radio-collared cougars were harvested just outside the study site boundaries (4 ♂, legal; 1 ♀, illegal).

Demographic Parameters

Age Structure.— Age estimates derived upon initial capture were pooled by sex and by site (Table 1). The age distribution of Monroe cougars (n=48) was weighted toward younger animals for both sexes (27 ♀, 21 ♂). However, the Oquirrh population exhibited greater variability in age with most females (n=18) in the middle and older age classes, whereas males (n=11) showed a similar pattern to those from Monroe (Figure 4). Results of the ANOVA indicated that both study site (df = 1, F= 12.6, P < 0.001) and sex (df = 1, F= 11.3, P < 0.001) had an effect on mean cougar ages. Further, the test suggested an interaction between sex and site (df = 1, F= 3.4, P = 0.07). Using Tukey’s pairwise comparisons to further explore this interaction (critical value = 3.74, family error rate =
0.05, individual error rate = 0.0105; Table 4), I found significant differences in mean female ages between sites \((P < 0.0105)\), and between females and males in the Oquirrh population \((P < 0.0105)\). Mean male ages did not differ between sites \((P > 0.0105)\), nor did males and females in the Monroe population \((P > 0.0105)\).

Figure 4. Age distribution of radio-collared cougars by sex, Monroe \((n=48)\) and Oquirrh \((n=29)\) Mountain study sites, Utah, 1996-2003.

Table 4. Cougar age structure (years) between sexes and study sites, Monroe and Oquirrh Mountains, Utah, 1996-2003.

<table>
<thead>
<tr>
<th>Site</th>
<th>Females</th>
<th></th>
<th></th>
<th>Males</th>
<th></th>
<th></th>
<th>Pooled</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>SE</td>
<td>n</td>
<td>Mean</td>
<td>SE</td>
<td>n</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Monroe</td>
<td>27</td>
<td>3.8</td>
<td>0.37</td>
<td>21</td>
<td>3.0</td>
<td>0.33</td>
<td>48</td>
<td>3.5</td>
<td>0.25</td>
</tr>
<tr>
<td>Oquirrh</td>
<td>18</td>
<td>5.9</td>
<td>0.52</td>
<td>11</td>
<td>3.3</td>
<td>0.42</td>
<td>29</td>
<td>4.9</td>
<td>0.43</td>
</tr>
</tbody>
</table>


_Cause-Specific Mortality._—Mortality on the Monroe site was predominantly human caused (84%), with legal harvest accounting for 79% and 67% of all human caused (n=24) and total mortality (n=29), respectively (Figure 5). Mortality on the Oquirrh site was highly variable (Figure 6). Human causes, including roadkill, comprised 44% of the total mortality (n=19), and of this legal harvest accounted for 50% of all human-caused mortality (n=8), but only 22.2% of the total. The proportions of human vs. non-human causes of mortality showed significant differences between sites ($\chi^2 = 7.5, P = 0.006$).

The second leading cause of death on both sites was intraspecific predation, comprising 3 mortalities on each site (Monroe = 10.3%, Oquirrhs = 16.7% of total mortality). On Monroe all intraspecific aggression occurred among adult females. On the Oquirrhs, 1 victim was a subadult male. Notably, another instance on the Oquirrhs was an adult female cannibalizing a subadult female. Two years later the survivor in this encounter was killed by an unidentified cougar. Other non-human causes (n=11) such as injury/starvation and prey capture, accounted for 26% of known mortality.

In addition to direct mortality, ≥ 8 kittens from 4 different litters on Monroe were orphaned when their mothers were killed due to legal harvest or depredation control. At least 3 of these kittens (single litter) are known to have died from starvation. On the Oquirrhs 1 orphaned kitten (mother hit by car) was killed to control depredation on a hobby farm in a suburb of Salt Lake City. Causes labeled as ‘unknown’ did not appear to be human related.
Figure 5. Cause-specific mortality among radio-collared cougars (n=29), Monroe Mountain study site, Utah, 1996-2003.

Figure 6. Cause-specific mortality among radio-collared cougars (n=19), Oquirrh Mountain study site, Utah, 1997-2003.
Survival.—Survival of adults and subadults varied among years and between sites (Table 5). On Monroe, survival (S_i) appeared to track harvest intensity fairly closely, ranging from a high of 1.0 at the beginning of the heavy harvest period, and declining to a low 0.36 ± 0.33 (95% CI) by the end of this period. Survival increased from 0.66 ± 0.31 to 0.90 ± 0.18 after per-capita harvest pressure dropped below 30% in 2002.

Survival on the Oquirrhs showed minimal variation, ranging from 0.63 ± 0.28 to 0.87 ± 0.23. Trends in survival mirrored those of density on both sites over the sample interval (Figure 7).

![Figure 7. Estimated annual survival rates (± SE) for radio-collared cougars, Monroe and Oquirrh Mountain study sites, Utah, 1996-2003.](image)
Table 5. Annual life history characteristics for all non-juvenile radio-collared cougars from the Monroe and Oquirrh Mountain study sites, Utah, 1996-2003.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Monroe</th>
<th></th>
<th></th>
<th>Monroe</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean</td>
<td>SE</td>
<td>Range</td>
<td>n</td>
<td>Mean</td>
</tr>
<tr>
<td>Survival</td>
<td>8</td>
<td>0.23</td>
<td>0.08</td>
<td>0.36 - 1.00</td>
<td>7</td>
<td>0.74</td>
</tr>
<tr>
<td>Fecundity</td>
<td>8</td>
<td>0.12</td>
<td>0.04</td>
<td>0.00 - 0.43</td>
<td>7</td>
<td>0.32</td>
</tr>
<tr>
<td>Density</td>
<td>8</td>
<td>0.73</td>
<td>0.26</td>
<td>1.1 - 3.2</td>
<td>7</td>
<td>2.8</td>
</tr>
</tbody>
</table>

_Fecundity._—Reproduction varied between sites and years (Table 5). The number of litters detected annually ranged from 0-9 on Monroe, and from 1-5 on the Oquirrhs. Fecundity rates did not differ statistically between sites (n=7 yrs, t = -1.05, P > 0.335). However, fecundity on the Monroe site tracked the population decline and included a zero detection rate in 2002, the year following the lowest population estimate, at which time there were at least 5 sexually mature females on the site. The lowest fecundity value for the Oquirrh population was recorded the year after a 50% reduction in elk numbers (Figure 8). This removal comprised primarily cows and calves, the sex/age classes most vulnerable to cougar predation (Murphy 1998). The sample of animals on the Oquirrh site was generally smaller (mean = 9.6 ♀ / yr) than on Monroe (mean = 15.7 ♀ / yr), which may have produced greater variability in fecundity estimates.

Litter sizes averaged 1.8 kittens on both sites. Based exclusively on the Oquirrh site using only kittens handled and marked, the sex ratio was even (8♀, 8♂).
Figure 8. Estimated annual fecundity rates (± SE) for adult cougars on the Monroe and Oquirrh Mountain study sites, Utah, 1996-2003. Estimates are based on the number of litters detected during winter tracking and capture events. Number of litters ranged from 0-9 on Monroe, and from 1-5 on the Oquirrhs.

Density.— Estimated high densities were similar between sites (Oquirrhs, 2.9, Monroe, 3.1), however trends in this parameter differed markedly (Figure 9). Density on Monroe showed a consistent decline during the years of heavy harvest (1997-2001), which leveled off when permits were reduced by 80% (2002-2003). Oquirrh density showed minimal variation over the entire study interval (Table 5).

Dispersal.— Several animals were captured and marked either just prior to, or during dispersal (Table 6). Four cougars (1♀, 3♂) moved from Monroe Mountain to neighboring mountain ranges 19–55 km distant. Two of these (1♀, 1♂) established residency in habitat adjacent to Monroe; 1 was recaptured and his collar removed (fate unknown); and 1 was harvested 42 km northeast on the Fishlake Plateau (Figure 10).
Figure 9. Annual non-juvenile cougar density (± SE) estimated from capture, tracking, and harvest, Monroe and Oquirrh Mountain study sites, Utah, 1996-2003.

Seven dispersals were documented on the Oquirrh site (2♀, 5♂), ranging in distance from 13-85 km (Figure 11). Of these, 3 (1♀, 2♂) settled elsewhere in the Oquirrh Mountains; 1 female moved to the Simpson-Sheeprock Mountains; 2 males moved to the Stansbury Mountains where they were harvested as transients; and 1 male dispersed across an 8-lane interstate and ≤ 6 km of city streets to the Mt. Timpanogos region of the southern Wasatch Mountains.
Table 6. Dispersal characteristics of subadult cougars from the Monroe and Oquirrh Mountain study sites, Utah, 1996-2003.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Cougar</th>
<th>Map ID*</th>
<th>Age¹</th>
<th>Captured</th>
<th>Dispersed</th>
<th>Direction</th>
<th>Distance</th>
<th>Fate²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monroe</td>
<td>M-10</td>
<td>1</td>
<td>1.5</td>
<td>3/26/1996</td>
<td>12/4/1996</td>
<td>125° SE</td>
<td>38 km</td>
<td>unknown</td>
</tr>
<tr>
<td>Monroe</td>
<td>M-14³</td>
<td>2</td>
<td>2</td>
<td>12/10/1996</td>
<td>4/7/1997</td>
<td>64° ENE</td>
<td>42 km</td>
<td>harvested 1/29/99</td>
</tr>
<tr>
<td>Monroe</td>
<td>F32b³</td>
<td>3</td>
<td>1.5</td>
<td>12/6/2001</td>
<td>Summer 2002</td>
<td>35° NE</td>
<td>55 km</td>
<td>established residency</td>
</tr>
<tr>
<td>Monroe</td>
<td>M-34³</td>
<td>4</td>
<td>2</td>
<td>12/7/2001</td>
<td>Spring 2002</td>
<td>250° WSW</td>
<td>19 km</td>
<td>established residency</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>F-63</td>
<td>1</td>
<td>0.5</td>
<td>2/10/1998</td>
<td>unknown</td>
<td>220° SW</td>
<td>85 km</td>
<td>harvested 3/21/02</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>M-64</td>
<td>2</td>
<td>0.5</td>
<td>2/10/1998</td>
<td>Spring 1999</td>
<td>180° S</td>
<td>28 km</td>
<td>depredation control 3/3/00</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>F-71</td>
<td>3</td>
<td>0.3</td>
<td>12/5/1998</td>
<td>unknown</td>
<td>215° SW</td>
<td>13 km</td>
<td>harvested 2/3/03</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>M-03³</td>
<td>4</td>
<td>1.5</td>
<td>1/28/2000</td>
<td>Summer 2000</td>
<td>270° W</td>
<td>28 km</td>
<td>established residency</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>M-07</td>
<td>5</td>
<td>0.7</td>
<td>1/14/2001</td>
<td>unknown</td>
<td>270° W</td>
<td>44 km</td>
<td>harvested 12/15/01</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>M-10</td>
<td>6</td>
<td>0.7</td>
<td>2/9/2001</td>
<td>unknown</td>
<td>268° W</td>
<td>46 km</td>
<td>harvested 12/30/01</td>
</tr>
<tr>
<td>Oquirrhs</td>
<td>M-21</td>
<td>7</td>
<td>1.5</td>
<td>4/12/2003</td>
<td>5/1/2003</td>
<td>135° SE</td>
<td>80 km</td>
<td>established residency</td>
</tr>
</tbody>
</table>

¹ Age (in years) upon initial capture
² At time of last contact or death
³ Captured during transient stage; natal range unknown
* See Figures 10, 11 for locations
Figure 10. Dispersal patterns and landscape connectivity, Monroe Mountain, Utah, 1996-2003 (for key, see table 6, column 3 map id).
Figure 11. Dispersal Patterns and landscape connectivity, Oquirrh Mountain study site, Utah, 1997-2003 (for key, see table 6, column 3 map id).
**Landscape Configuration**

The 2 study sites exhibited similar perimeter-area indices, but notable differences in connectivity and perimeter permeability (Table 7). Currently, no substantial movement barriers exist along the perimeter of Monroe Mountain, and in general, the unit is well connected to other habitats of similar quality within the Southern Mountains ecoregion (Figure 10).

In contrast, only 5% of the Oquirrh's perimeter is connected to neighboring habitat and approximately 40% is impermeable to cougar movement. Movement barriers include the southern shore of the Great Salt Lake (7 km), the Salt Lake metro area (50 km), and a heavily traveled segment of Interstate 15 (2 km), which bisects the Traverse Mountains (Figure 11). The remaining 55% grades into salt desert scrub communities offering little vegetative cover or surface water (West 1983). Additionally, residential development emanating from the Salt Lake - Provo metropolitan epicenter is much greater around the Oquirrh site.

Table 7. Measures of landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Monroe</th>
<th>Oquirrhs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perimeter (km)</td>
<td>178</td>
<td>150</td>
</tr>
<tr>
<td>Area (km²)</td>
<td>1300</td>
<td>950</td>
</tr>
<tr>
<td>Perimeter : Area</td>
<td>0.137</td>
<td>0.157</td>
</tr>
<tr>
<td>Greatest interpatch dist. (km)</td>
<td>7</td>
<td>25</td>
</tr>
<tr>
<td>Perimeter impermeable (%)</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>Perimeter connected (%)</td>
<td>33</td>
<td>5</td>
</tr>
<tr>
<td>Width connective habitat (km)</td>
<td>7-21</td>
<td>2-4.5</td>
</tr>
</tbody>
</table>
Overall, the Oquirrh exhibit much thinner and more tenuous connectivity to neighboring patches of generally poorer quality (i.e. lower primary production); a pattern typical of basin and range topography (Figure 1). This topographic fragmentation combined with anthropogenic fragmentation in the foothills and valleys around the site render this area susceptible to isolation (see Beier 1995).

**Harvest Rates and Distribution**

*Study Site Harvest Rates.*—Mean harvest rates on the study sites were 0.93 cougars and 0.21 cougars / yr / 100 km$^2$ for the Monroe (hunted) and Oquirrh (protected) populations, respectively (Table 8). The mean annual harvest rate on Monroe coincided with a > 60% decline in density over the period 1996-2001, while the mean annual harvest rate (any and all human-caused mortality) on the Oquirrhs coincided with a static density over the same interval.

Table 8. Cougar harvest rates (sum of all human-caused mortality), Monroe and Oquirrh Mountain study sites, Utah, 1996-2001.

<table>
<thead>
<tr>
<th>Hunting season</th>
<th># cougars killed / 100 km$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Monroe</td>
</tr>
<tr>
<td>1996</td>
<td>1.08</td>
</tr>
<tr>
<td>1997</td>
<td>1.38</td>
</tr>
<tr>
<td>1998</td>
<td>1.31</td>
</tr>
<tr>
<td>1999</td>
<td>0.54</td>
</tr>
<tr>
<td>2000</td>
<td>0.84</td>
</tr>
<tr>
<td>2001</td>
<td>0.46</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>0.93 ± 0.16</td>
</tr>
</tbody>
</table>
Statewide Harvest Rates.—In total, 2,438 legal kills were assigned coordinates. Approximately 10% of the total available harvest data were excluded from analysis due to the lack of identifiable place names or the occurrence of duplicate place names within a management unit. A total of 2,328 kills fell within watersheds ≥ 100 km²; and 1,198 fell within the 75 largest watersheds (≥ 500 km²; Figure 12). Within large watersheds harvest rates were highly variable, with 13.4% (n=10) exhibiting rates ≤ Oquirrh harvest rates (0.21); 74.6% (n=56) exhibiting harvest rates ≥ Monroe (0.93); and the other 12% (n=9) falling between these 2 benchmarks (Table 9). Of those watersheds equaling or exceeding Monroe harvest rates, 41.1% (n=42) were 1-1.9 times greater; 48.2% (n=27) were 3-4.9 times greater; and 7.1% (n=6) exceeded Monroe by 5-8.1 times. Overall, cougar populations inhabiting approximately 59% of total habitat were exploited at rates of at least 0.93 cougars / yr / 100 km².

Table 9. Statewide harvest rates (cougars killed / yr / 100 km²) for watersheds ≥ 500 km² (n=75), 1996-2001.

<table>
<thead>
<tr>
<th>Harvest rates</th>
<th>n</th>
<th>Mean</th>
<th>SE</th>
<th>Range</th>
<th>% Total</th>
<th>Population trend¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤ 0.21</td>
<td>10</td>
<td>0.04</td>
<td>0.02</td>
<td>0.00-0.15</td>
<td>13.4</td>
<td>Stationary</td>
</tr>
<tr>
<td>0.22 to 0.92</td>
<td>9</td>
<td>0.49</td>
<td>0.06</td>
<td>0.25-0.72</td>
<td>12.0</td>
<td>Undetermined</td>
</tr>
<tr>
<td>≥ 0.93</td>
<td>56</td>
<td>2.94</td>
<td>0.24</td>
<td>0.98-8.18</td>
<td>74.6</td>
<td>Declining</td>
</tr>
</tbody>
</table>

¹Estimate based on study site means
Cougar harvest varied by location within watersheds. Density estimates portray harvest as an even distribution within watersheds, however some watersheds showing high levels of exploitation contained areas of little or no harvest, the effects of which were masked by this technique (e.g. Zion National Park; Figure 13).
Figure 12. Statewide harvest rates for watersheds $\geq 100$ km$^2$ (cougars killed / yr / 100 km$^2$). Gray represents unsuitable habitat; Yellow is agriculture, and Black represents urban areas.
Figure 13. Statewide cougar harvest rates by drainage, 1996-2001.
DISCUSSION

Influence of Harvest on Population Dynamics

The simultaneous monitoring of these populations revealed insights to the impacts of sustained harvest on cougar population dynamics. Demographic characteristics between sites differed notably and were consistent with predictions for different levels of exploitation.

*Population Dynamics.*—Murphy (1983) in Montana and Ashman et al. (1983) in Nevada documented harvested cougar populations remaining numerically stationary under 25-32% removal rates. Based on these observations, Ashman et al. recommended that harvest not exceed this level in order to maintain mortality commensurate with recruitment. Logan et al. (1996) estimated that harvest exceeding 28% of the standing population for 3 years could reduce the population by 50%. Results from this study support these contentions. Cougar removal (harvest, depredation control, and poaching) on Monroe Mountain ranged from 17.6 to 54.5% of the non-juvenile segment of the population, and exceeded 40% for 4 of 5 years of high per-capita hunting pressure. Females comprised 32% of the harvest, but 100% of depredation control and poaching mortality, resulting in a minimum of 4 orphaned litters. During this period the population declined by > 60%. Concurrently, the Oquirrh Mountain population remained stationary, despite a large reduction in available prey biomass (UDWR, unpublished data).

A large proportion of the statewide cougar population appeared to be exploited at rates equal to or exceeding those measured on Monroe Mountain. The results suggested that
management objectives to reduce cougar densities during the sample interval were most successful in cougar habitat within the Wasatch cordillera. If density trends on Monroe are extrapolated to watersheds exhibiting similar harvest rates, the statewide population was likely reduced by the turn of the 21st century. However, several large watersheds open to hunting but displaying very light harvest levels stood out, and may represent de facto refugia. The greatest of these was the largely roadless section of the Tavaputs Plateau straddling Desolation Canyon (~2,400 km²). Other regions measuring ≥ 500 km² exhibiting low harvest rates included the Kaiparowitz Plateau, western Raft River Mountains, portions of the Abajo Mountains, the southern Deep Creek Mountains, the Wasatch Front east of Salt Lake City, and the southeastern Wasatch Plateau. In addition, several National Park units show promise as cougar refugia, including Zion, Capitol Reef, and Dinosaur.

Among the most heavily harvested watersheds, variability in harvest intensity was exceptional. Seventy-five watersheds ≥ 500 km² exhibited harvest rates ranging from 0.93 to 8.2 cougars/yr/100 km². This pattern suggests either significant discrepancies in cougar density and productivity, or differential vulnerability to harvest by location. Spatial factors influencing cougar vulnerability warrant further investigation.

Two biases are inherent in this technique. First, any presumed harvest impacts are based on cougar densities measured on the Monroe and Oquirrh mountain study sites. These values may not reflect the range of densities found across the state over a variety of habitat conditions. Average cougar densities on the study sites were similar to each other (Table 5), but were relatively high compared to densities recorded elsewhere in Utah.
(Lindzey et al. 1989, Lopez-Gonzalez 1999). The harvest rate is static and therefore if a given watershed contained a higher cougar density, then this rate would have a smaller impact on the population; conversely, if density were lower, then the same harvest rate would have a greater impact. Secondly, harvest rates were calculated based solely on hunting records and do not reflect mortality from other human causes such as depredation control, roadkill, or poaching. Therefore, the results of this analysis likely underestimate the true harvest rates and any subsequent impacts on population dynamics.

*Demographic Comparisons.*—Age structure differed significantly between sites, with the Monroe population composed primarily of subadults and completely lacking any individuals > 8 years old. The Oquirrh population exhibited a higher mean age among females, a smaller proportion of subadults, and the presence of several individuals > 10 years of age. The dearth of transient females may reflect productivity outside the study site and/or movement constraints. Age distribution of males did not differ between sites, suggesting either: (1) males and females had a fundamentally different age structure in the general population or, (2) the unhunted portion of the Oquirrhs was smaller than a typical male home range, and thus conferred only temporary protections. These findings were consistent with those of Hopkins (1989), whose unhunted study population exhibited higher mean ages than those measured in exploited populations; and with Anderson (2003) who noted the mean female age declined by 50% following a second year of heavy harvest in his treatment population.

Cause-specific mortality clearly reflected differences in management. Removal by humans accounted for 84% of known mortality among marked cougars on Monroe, but
only 42% on the Oquirrh, despite proximity to the densest human population in the state (see Linnell et al. 2001). Though humans represented the single greatest source of mortality for animals traveling outside the Oquirrh study site, the absence of harvest within the study area suggested that the Camp Williams - Kennecott properties collectively acted as a functional refuge within the Oquirrh Mountains. Due to their smaller home ranges and restricted movements, resident females were the primary beneficiaries of this protected status. In addition, survival, fecundity, and density were all negatively associated with sustained high per-capita harvest pressure on Monroe Mountain. Conversely, with the exception of fecundity, these measures remained fairly constant over the same interval on the Oquirrh site. It is important to note, this study was initiated at a time when cougar populations in many parts of the state were slated for reductions. Although it is possible that other factors contributed to the dynamics observed in the Monroe Mountain cougar population, the prevalence of human caused mortality, lack of starvation as a mortality cause, and an increasing elk population (K. Rasmussen, Fishlake National Forest, unpublished data) suggested that harvest was the proximate cause of the decline.

The consequences of sustained heavy harvest may not be limited to numeric changes in the population. High mortality has implications for fecundity. Fecundity on Monroe tracked per-capita harvest pressure with a 1-year lag. I found no support for the hypothesis of compensatory reproduction under increased harvest levels, as has been noted for several monogamous carnivores (Knowlton 1972, Frank and Woodroffe 2001, McNay et al. 2003). Results from several comparative studies supported these
conclusions. In his examination of harvest impacts on African lions, Smuts (1978) found a post-harvest increase in the proportion of subadult males in the population, which was negatively correlated with birth rates and kitten survival. However, this effect was not apparent when harvest was light and selective enough to be compensatory. Similarly, Knick (1990) examined demographics in exploited and unexploited bobcat (*Lynx rufus*) populations in Idaho and found a disproportionate number of subadult males and lower productivity in the harvested population. Wielgus and Bunnell (2000) compared exploited and unexploited brown bear populations and observed similar results. Wielgus and Bunnell hypothesized that hunting adult males facilitated the influx of immigrant males, thus depressing recruitment through direct (infanticide) and indirect means (female avoidance of food rich habitats to avoid unfamiliar males).

In general, direct parental investment is low among polygynous male carnivores. However the hypothesized function of male territoriality in these species is to indirectly increase offspring survival by excluding non-sire males from the natal range (Bertram 1975, Ross and Jalkotzy 1992). Infanticide is a common strategy for optimizing male fitness in polygynous species (Bertram 1975, Hrdy 1979, Packer and Pusey 1983) and is well documented in cougar populations (Hornocker 1970, Hemker et al. 1986, Anderson et al. 1992, Spreadbury et al. 1996, Pierce et al. 1998, Lopez-Gonzalez 1999). Due in part to the small sample of marked kittens, I did not observe this behavior, however turnover of resident males appears to be the mechanism promoting infanticide in other carnivores (Packer and Pusey 1984, Smith and McDougal 1991, Swenson et al. 1997), and is hypothesized to be a greater mortality factor in hunted populations because of this
(Ross and Jalkotzy 1992, Wielgus and Bunnell 2000). In the Monroe population, low fecundity rates could have been the product of several factors including the loss of mature breeders, extended birth intervals, and decreased kitten survival. Hemker et al. (1986) noted that kitten survival in exploited populations has not been adequately quantified.

Heavy harvest and subsequent social instability may have reduced the reproductive capacity of the Monroe population and therefore its ability to compensate losses. The female segment of this population was comprised of animals that had made little or no reproductive investment the population, while the typical female on the Oquirrh site had already replaced herself numerically. Additionally, similar to the findings of Lindzey et al. (1992), intraspecific aggression on Monroe still occurred under the lowest densities, and exclusively among adult females. Results indicate annual harvests exceeding 30% of the adult population consisting of 42% females, and carried out continuously for > 3 years may be able to reduce density, impact fecundity, and skew age structure.

**Harvest Dynamics and the Regional Metapopulation**

Metapopulation structure has been cited as a possible explanation for the genetic organization of Basin and Range cougar populations, and those severed by human activity in California (Loxterman 2001, Ernest et al. 2003). Accordingly, the metapopulation concept has been proposed as a framework for managing cougar populations by various authors (Beier 1996, Sweanor et al. 2000, Maehr et al. 2002, Laundré and Clark 2003). However, at present there exists no consensus among researchers on the degree to which cougars conform to metapopulation assumptions and
mechanisms under particular environmental conditions (Anderson 2003, Ernest et al. 2003).

Whereas the metapopulation model focuses on the dynamics resulting from the size and configuration of habitat patches, the source-sink model emphasizes the variability of survival and fecundity parameters within and among patches (Ritchie 1997). This model infers fitness and recruitment patterns over a productivity gradient, connected by density-dependent dispersal events (Pulliam 1988). Demographically, the Monroe and Oquirrh populations approximate the sink-source archetypes respectively, albeit as a result of exploitation levels rather than overall habitat quality (Van Vuren and Smallwood 1996). When harvest and its apparent impacts are considered, the Monroe population exhibited sink-like mortality despite its association with highly productive habitat. Notwithstanding low kitten production, each winter new animals, primarily subadult males, were detected on the site. It is possible some of these individuals were resident progeny, however mammalian dispersal patterns tend to be male-biased (Greenwood 1980, Lindzey et al. 1992, Ross and Jalkotzy 1992, Sweanor et al. 2000), suggesting that most of these animals were immigrants. Low productivity and high immigration rates are the essence of a sink population.

In contrast, the Oquirrh population exhibited higher productivity, nearly static density and emigration of resident progeny. No marked female kittens were ever detected as adults on the site, suggesting either high kitten mortality, or a high rate of egress. This is indicative of a population, which at current prey densities, has saturated available habitat and is contributing to recruitment in neighboring demes. Indeed, 5 kittens (2♀, 3♂) born
on the site were later killed elsewhere in the Oquirrhs or on neighboring mountain ranges up to 85 km distant. Solely based on age (4 yrs) the female emigrants could have raised one litter to independence prior to being harvested, while the males were killed immediately upon leaving their natal ranges, thereby subsidizing the harvest in adjacent units. On the Oquirrh site density-dependent reproduction appeared to discourage philopatry and encourage dispersal among resident progeny of both sexes suggesting a source-like population structure.

When the prevailing harvest rate is considered a component of habitat quality, then a spatially clumped harvest distribution can promote source-sink dynamics. The result can be an immigration gradient directed toward habitat patches such as Monroe Mountain, where strong connectivity coupled with low population density make the site what has variously been called an "attractive sink" (Delibes et al. 2001) or "ecological trap" (Kokko and Sutherland 2001). That is, an environmentally high quality habitat that exhibits sink-like mortality patterns. These sites represent examples of populations exhibiting substantially different dynamics simultaneously within the metapopulation. However source-sink characteristics may be transitory depending on how the predominant management regime interacts with habitat productivity and connectivity in and around the focal population.

Both the metapopulation and source-sink models have been used to describe population dynamics for a host of other exploited or patchily distributed carnivores (Bailey et al. 1986, Knick 1990, Jackson and Fox 1995, Noss et al. 1996, Delibes et al. 2001, Ferreras 2001, Johnson et al. 2001, Mauritzen et al. 2002). Cougars occur at low
population densities in patches of varying size, quantity, distance, and productivity, yet exhibit a spatially flexible social system and strong dispersal abilities (Pierce et al. 1998, Sweanor et al. 2000), making the delineation of discrete populations difficult (Pierce and Bleich 2003). Source-sink dynamics may be more amenable to field evaluation than the extinction / recolonization events that define classic metapopulations (Levins 1969).

Despite deviations from theoretical assumptions, these concepts show strong potential as a tool in broad-scale cougar management in Utah and other Basin and Range and Rocky Mountain states. A more liberalized model accounting for source-sink dynamics among demes but within a metapopulation context may provide the appropriate scale and framework to manage cougar populations regionally (Harrison 1994, Wiens 1996, Drechsler and Wissel 1998).

**Factors Influencing the Rate of Population Recovery**

Several removal experiments have been conducted on cougar populations to examine the demographic mechanisms and time scales of population recovery. Notable among these were the studies conducted in southern Utah by Lindzey et al. (1992), and in New Mexico by Logan and Sweanor (2001). These investigators found that, following density reductions, female recruitment was achieved via philopatric behavior or diffuse dispersal, while male recruitment was solely the product of immigration (Lindzey et al. 1992, Logan and Sweanor 2001). Although these studies provided valuable insights into population responses to disturbance, temporally they were conducted over one season with no subsequent removals. The Monroe study population however, had only a 7-
month annual window during which harvest pressure was reduced to depredation control and poaching. In addition to rest periods, large sanctuaries spatially buffered the removal zones in those experiments (Utah ~ 2,600 km², New Mexico ~ 1,300 km²). In both studies, no movement barriers divided treatment and control areas. In stark contrast, Monroe Mountain was surrounded by units with similar harvest intensities. Therefore, recovery times noted by Lindzey et al. (1992) and Logan and Sweanor (2001) should be considered best-case scenarios given the temporal and spatial refugia provided.

Population recovery following disturbance may progress from *numerical* to *functional*. The studies noted above suggested numeric recovery, i.e. increases in density, can occur within 2-3 years under complete protection. This is achieved primarily via immigration of subadult males and philopatric behavior of resident female progeny (Laing and Lindzey 1993, Anderson 2003). During this period, the population may exhibit a high rate of increase, but reproduction may lag, due to the lack of established breeders, Allee effects (Kokko and Sutherland 2001), long birth intervals, and low kitten survival, as an artifact of social instability.

Functional recovery implies not simply an increase in density, but rather a shift to female-biased sex ratios in the resident segment of the population, and accompanied by higher productivity and kitten survival. This involves a stabilization of social relationships and a decrease in the variability of vital life history rates. Anderson (2003) speculated that one-time removals might not be as socially disruptive as harvest sustained over multiple years, as the former would be roughly analogous to normal resident
turnover. Presumably a compensatory harvest would not necessitate the numeric phase of recovery, but this hypothesis awaits further investigation.

It has been hypothesized that where habitat connectivity is high, moderate harvest levels may facilitate an increase in cougar density, because the removal of residents may induce a “vacuum effect” in which multiple transients vie for the open space (Shaw 1981, Logan et al. 1986a). Results of this research lend limited support to this argument. A modest increase was observed in the relative proportion of subadult males within the population subsequent to removal of resident males, while the absolute density of cougars on the site decreased. Additionally, many of the marked subadult males left Monroe within 6 months of capture, suggesting any increase was temporary. In general, males tend to disperse farther than females (Sweanor et al. 2000, Maehr et al. 2002), remain transient longer (Cunningham et al. 2000, Maehr et al. 2002), and are less tolerant of other males (Logan and Sweanor 2001). Conversely, females often exhibit philopatric behavior (Logan and Sweanor 2001, Maehr et al. 2002), reproduce at an earlier age than males (Murphy 1998), and tolerate spatial overlap with other females (Pierce et al. 2000). Therefore, the transient segment of the cougar population is likely to be male biased (Hansson 1991). The removal of resident males provides habitat vacancies that may be contested by multiple immigrants, thereby temporarily increasing the proportion of males in the population (Logan et al. 1986a), but not the overall density of males, or of the population in general.

In addition to fecundity, kitten survival, and harvest rates in adjacent demes, landscape connectivity facilitates demographic continuity, and thus is an important factor in
population recovery. For example, if a source population is near a low-density site and habitat connectivity is sufficient to facilitate movement between sites, then immigration recruitment of both sexes will influence the recovery rate (Lindzey et al. 1992, Taylor et al. 1993, Logan and Swcanor 2001). Lindzey et al. (1989) hypothesized that population recovery may be delayed in areas where transient ingress is restricted. Strong connectivity is likely the primary reason transient animals were detected on Monroe each winter, acting as a negative feedback to buffer the population from further declines (Brown and Kodric-Brown 1977, Stacey et al. 1997), but not contributing to productivity.

Research conducted by Beier (1996) on a small semi-isolated cougar population in suburban southern California corroborates this idea. Reproduction in that study population subsided for 12 months due to Allee effects (Padley 1990, cited in Beier 1996). This site represented an extreme in terms of isolation, having been almost completely surrounded by urban sprawl, reducing connectivity to a few undeveloped strips acting as movement corridors (Beier 1995). Landscape connectivity, through the mechanism of reduced immigration, was the primary factor influencing the tenuous persistence of the population. Due to its proximity to the largest urban area in the state and concomitant growth rate, Beier's results have strong implications for the Oquirrh Mountain cougar population.

Conclusions

The Southern Mountains ecoregion is defined by growing season precipitation and strong inter-range connectivity. Low human population density, slow economic growth,
and the predominance of publicly owned land indicate anthropogenic fragmentation is not as grave a concern in this area as is elsewhere in the state. Although the Monroe population appeared demographically fragile, under a more conservative management regime it is likely that this population would recover rapidly and exhibit densities and productivity commensurate with prey abundance (Pierce et al. 2000), and conceivably could act as a source population.

Conversely, cougar habitat in the Great Basin exhibits weak connectivity among sparsely distributed semiarid desert ranges. Urban sprawl, interstate highways, and the Great Salt Lake function as barriers to animal movement on the north and east sides of the Oquirrh range, while to the west, desert basins up to 25 km in width separate suitable habitat patches. Overlaid on this landscape, urban development driven by the expansion of the Salt Lake metro area is further isolating the Oquirrh range. Although this population appeared demographically robust, it was small and therefore more susceptible to stochastic declines. In the event of a reduction, the lack of connectivity could hinder recovery and could induce sink-like characteristics.

Heavy harvest not only can reduce density, but in so doing can alter the demographic structure of the population to one that is younger, less productive, and socially unstable. When harvest patterns are examined at a broader scale, differential vulnerability can result in locally variable survival and recruitment rates leading to source-sink dynamics. Recovery of heavily harvested populations will likely be influenced by the spatial arrangement of sources and sinks and the relative degree of habitat connectivity between them. Accounting for these patterns should be considered an integral component of
effective management schemes. The metapopulation concept addresses species distributions and focuses on the spatial discontinuity and variability in size and quality of habitat patches, thus offering a model for the management of species’ whose populations exhibit dynamics on large spatial and temporal scales. In the absence of robust population estimators, managers should consider a geographically explicit, multi-year strategy to the management of cougar populations by identifying areas of chronic overexploitation and *de facto* refugia, and adjusting harvest strategies that utilize their spatial arrangement.
MANAGEMENT IMPLICATIONS

If density reductions are the management objective for a given unit, then a harvest rate \( \geq 40\% \) of the population / year for \( \geq 3 \) years, consisting of 1F : 1.5M may result in substantial reductions. If the subsequent objective is to recover the population to a level near carrying capacity, the unit should be rested for \( \geq 4 \) years in order to insure both numeric and functional recovery. Four years would allow a newborn female to mature and complete one reproductive cycle (1 litter of kittens nurtured from birth to independence) thus offering an appropriate schedule for minimizing harvest. Managing these areas as pursuit-only or as trophy units under a rest / rotation cycle may prove more politically attainable than the biologically preferred alternative of complete closure.

Whereas populations are most sensitive to the loss of adult females (Lindzey et al. 1992), they are least sensitive to the loss of subadult (often transient) males. Hunting related mortality will have the greatest compensatory effect when focused on this cohort and away from adult residents of either sex. It is important to note however, that transient males are responsible for most of the genetic interchange occurring within a metapopulation, and in isolated populations this function may play a more important role in population persistence (Sweanor et al. 2000). Males of any age are more expendable than females, however in contrast to the population dynamics of ungulate species, the loss of resident males may not be completely benign. Evidence from other studies suggests that resident adult males may indirectly benefit the survival of their own offspring by excluding transient males from the natal range.
Human-caused mortality is the only variable over which managers have immediate control. Survival in the Monroe population increased from 0.36 to 0.66 to 0.90 after a 66% decrease in the number of permits issued over 2 hunting seasons. Although low harvest may be correlated with higher survival, reproduction may lag until residency status and social relationships among members stabilizes. Results derived by Lindsey et al. (1992) and from this study suggested that density-independent sources of mortality such as failed predation attempts can be additive when densities are low. Additionally, intraspecific predation did not appear to subside under lower densities, but may have shifted from a semi-compensatory focus on subadult males to an additive effect when directed at adult females. The motivations for this behavior are unknown at this time. These data showed that known reproductive females suffered the full brunt of poaching and depredation-control mortality. Female sub-quotas offer a means of reducing this effect by encouraging hunter selectivity for males.

In addition to density reductions, heavy harvest may have measurable impacts on cougar demographic structure. Sustained harvest tends to result in a higher rate of kitten orphanage. Two consequences of this are the potential loss of reproductive cohorts, and a probable increase in the proportion of nuisance animals (urban or rural depredators). Due to the unpredictable movement and feeding habits of this cohort, non-selective density reductions may not always be the best means of addressing depredation concerns in all areas.

Observed patterns of dispersal and recruitment suggest a source-sink type of population structure due in part to spatially variable management strategies. Further,
harvest rates and dynamics extrapolated from Monroe Mountain suggest the statewide population experienced significant declines during the late 1990s. This indicates that density reductions will be most attainable in core cougar range situated most closely to human population centers.

Initially, numerical recovery of heavily harvested populations may depend more on immigration than on in situ reproduction, indicating harvest levels on adjacent units can be influential in how soon a depressed population recovers. Managers should interpret the recovery times calculated by Lindzey et al. (1992) and Logan and Sweanor (2001) with caution. These estimates were derived under optimal conditions where both temporal and spatial refugia were immediately available to facilitate and subsidize recruitment. Consequently, what should be gathered from these studies is the importance of refugia surrounding or adjacent to the focal unit, and/or hunting reductions following harvest. Protected areas should be at least as large as the control zone and of commensurate habitat quality. In sum, management should account for spatial patterns of harvest and how these patterns may interact with cougar recruitment behavior under various states of social stability. Until a set of reliable and repeatable enumeration techniques are developed, Zone Management as proposed by Logan and Sweanor (1998) or some variant of that concept (McCullough 1996), may provide an alternative means of managing for statewide cougar population persistence.
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