THE GARNET RANGE MOUNTAIN LION STUDY

Characteristics of a Hunted Population in West-Central Montana

Prepared by:
Hugh Robinson and Rich DeSimone

Montana Fish, Wildlife & Parks

Wildlife Restoration

Final Report 2011

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Montana Fish, Wildlife and Parks
Wildlife Division
Helena, Montana 59620

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Cover Photo Credit:

Uncollared female lion treed south of Missoula in the Missoula Special Management Area.
(Photo courtesy of Bob Wiesner)

AUTHORS

Hugh Robinson. Hugh has been involved in mountain lion research in British Columbia, Washington, and Montana since 1996. Hugh received his Master's and Ph.D. from Washington State where he studied the population dynamics of mule deer, white-tailed deer, and mountain lions. He is currently a postdoctoral researcher with the Montana Cooperative Wildlife Research Unit at the University of Montana, Missoula MT.

Richard DeSimone. Rich received his Bachelor and Master's degrees from Montana State University in Bozeman. He spent his entire career as a Research Biologist with MFWP starting in 1976 and retiring in 2010. His research focusing on mountain lion survival in the Blackfoot Drainage began in 1997.

Hugh Robinson and Rich DeSimone

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FOREWARD

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For much of the history of settled Montana, mountain lions had it tough. Their prey was driven to all time historic low population sizes by the end of the 19th and early 20th centuries. Subsequently, lions were considered sufficient threats to property and safety that they were purposefully persecuted, indiscriminately. In fact, the bounty on mountain lions was eliminated in Montana only two generations ago, in 1962.

The future of lions began to change in 1971 when they were first classified as a game animal. This paved the way for recovery of mountain lion populations, which was successful to the point of generating more conflict with humans by the late 1980's and early 1990's, including a human fatality near Missoula. In response to these conflicts, lion harvest quotas were increased substantially in many parts of Montana.

This in turn resulted in an outcry from lion conservationists, primarily lion hunters and houndsmen, who were upset with the resulting low mountain lion numbers and the general lack of detailed information about mountain lions in Montana. As a result of this controversy, Montana Fish, Wildlife and Parks completed an Environmental Impact Statement in 1995 summarizing the Montana lion management program and data, which has served as a basis for lion management in Montana ever since.

It was in the midst of this historical context and contemporary controversies that the Garnet lion research project began in 1997. Recognizing limitations in our current knowledge, a primary focus of the research was to reliably quantify how public harvest of mountain lions impacts their population dynamics. Also recognizing practical realities of tracking populations of the elusive cats over relevant scales for conservation, the project aimed to evaluate several proposed methods for monitoring lion populations that could be incorporated into real-world lion management programs. These two objectives were agreed upon by all sides of the controversy, as everyone was in search of reliable information, and the project thus has served as a common ground for disparate interests since it began.

Despite the controversy and the daunting information needs, this project can only be viewed as a success. This is the final product of the research effort, and these pages represent the very best of applied wildlife research. Contained within are data meticulously gathered by incredibly dedicated staff spending long hours in the field enduring all seasons in western Montana, for 10 long years. The local community, houndsmen, and hunters were involved in all aspects of the project from inception through completion. Rigorous and reliable analysis methods have been brought to bear on these hard-won data, and the results are solid and trustworthy.

As such, this final report will serve as a cornerstone for future mountain lion management and conservation in Montana for years to come. These results are already being applied to lion management across the state by wildlife biologist and managers. The results have further identified other information gaps and research needs that are being pursued currently. And, at long last, the results will be front and center in coming lion management planning for Montana.

Mike Thompson

Mike Thompson
Montana Fish, Wildlife and Parks
Region 2 Wildlife Program Manager
Missoula, Montana

Justin Gude
Montana Fish, Wildlife and Parks
Wildlife Research and Technical Services Manager
Helena, Montana

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Kitten of radio collared female F35 at 5 months of age. *(Photo courtesy of Melanie Trapkus)*

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EXECUTIVE SUMMARY

Large carnivores pose a particular challenge in wildlife management. Their importance in ecosystem function is increasingly well documented, while at the same time their potential for conflict with humans is high, resulting in often divergent public opinion and management objectives. Carnivores are widely hunted for recreation, population control, and to reduce conflict, both direct and indirect with humans.

Uncollared female mountain lion treed south of Missoula in the Missoula Special Management Area. (Photo courtesy of Bob Wiesner)

In Montana and western North America, mountain lion populations increased and expanded their range during the 1990s. This resulted in more interactions between lions and humans and the general public became more aware of mountain lion presence. Public acceptance of mountain lions was found to vary with lion population growth, and perceived risk.

Increases in mountain lion distribution and abundance resulted in public concern over human safety, increased livestock and pet depredation, and the effects of predation on ungulate populations. In most jurisdictions in western North America, including Montana, these concerns have been addressed with increased harvest. In turn, increased harvest rates raised concerns among other sectors of the public regarding the potential biological impacts of overharvest. Previous

Large carnivores pose a particular challenge in wildlife management.

The southern portion of the Garnet Mountains looking southwest down Cramer Creek toward the Clark Fork River. (Photo courtesy of Melanie Trapkus)

Rocky area south of junction of North Fork and main Blackfoot River south of Ovando. (Photo courtesy of Melanie Trapkus)

research has shown that mountain lion populations have a high level of resiliency to harvest and can recover quickly; however, some jurisdictions have also seen large oscillations in population levels, likely due to overharvest (e.g. British Columbia and Washington).

In response to public concerns, Montana Fish Wildlife and Parks undertook a 9 year mountain lion research program beginning in 1997.

In response to public concerns, Montana Fish Wildlife and Parks undertook a 9 year mountain lion research program beginning in 1997 focused within Montana's hunting district 292. The goal of this research was twofold:

1) **Document population characteristics of a hunted mountain lion population in the mountain/foothill habitat type including density, composition, productivity, mortality, recruitment, dispersal and home range size.**
2) **Evaluate the accuracy of track surveys and other management applicable techniques to detect trend in mountain lion abundance.**

We investigated population effects of harvest on mountain lions using a pseudo-experimental before-after-control-impact (BACI) design. We achieved this through 3 years of intensive harvest followed by a recovery period. In December 2000, after three years of hunting, approximately two-thirds of district 292 was closed to lion hunting which effectively created a refuge, representing approximately 12% (915 km^2) of the total Blackfoot watershed (7,908 km^2). Hunting continued in the remainder of the drainage, but harvest levels declined between 2001 and 2006 as quotas were reduced.

From January 1998 and December 2006, a total of 121 individual mountain lions were captured 152 times, including 82 kittens, and 39 juveniles and adults. Of these, 117 individuals were collared and monitored for habitat use and survival. On average animals were monitored for 502 days (approximately 16 months) with a range of 7 to 3231 days, with males remaining on the air for shorter periods ($\bar{X}$ = 284 days) than females ($\bar{X}$ = 658 days).

Our study population displayed the effects of harvest that have also been shown elsewhere. While hunting directly reduced survival, reproductive population parameters such as litter size, birth interval, maternity, age at dispersal and first breeding, as well as home range size and overlap where not significantly affected.

Hunting was the main cause of mortality for all age and sex classes across the study period, accounting for 36 of 63 mortalities documented. This was followed by illegal mortalities, natural, vehicle collisions, depredation, and unknown causes. Across the study period, any lion in the Blackfoot watershed had, on average, a 22% annual probability of dying due to hunting. We found human harvest to be an additive mortality source (i.e. hunting mortality was not compensated for by increased survival of remaining individuals).

Population modeling suggested that the lion population in the greater Blackfoot watershed was declining annually between 8 and 12% prior to the protection of the Garnet study area in 2001, but recovered to near 1998 levels by the end of the study in 2007. Recovery was attributed to the protection of the Garnet area which allowed dispersal from the Garnet to the remainder of the watershed, and reduced quotas in the hunted portions of the watershed beginning in 2004. Sensitivity analysis showed that female survival and maternity were most influential on population growth.

Life-stage simulation analysis (LSA) demonstrated the effect of hunting on the normal population dynamics of mountain lions. Evolutionary theory points to survival and fecundity as defining fitness. As a long-lived species, mountain lion populations should show the lowest degree of variability in the vital rate that contributes most to fitness, namely adult survival. In our non-hunted population, reproduction (kitten survival and maternity) accounted for approximately 71% of the variation in growth rate while adult female survival accounted for 22%. Hunting reversed this adaptive strategy increasing the reliance of population growth on adult female survival (40% of the variation in population growth), and away from reproduction (17%).

Capture, based on intensive field efforts (i.e. searching for tracks in snow during winter) remains the best method of census for mountain lions. However, this method is prohibitively expensive and time-consuming. A recent survey of state game agencies found that obtaining a method of quantifying mountain lion populations and trend was a research priority for most jurisdictions. The need for easily-obtained and inexpensive indices is apparent, however our results add to a growing body of evidence that have found these techniques lacking. Most of the indices we evaluated were

Capture, based on intensive field efforts (i.e. searching for tracks in snow during winter) remains the best method of census for mountain lions.

Radio-collared subadult female F55 near Chamberlain Creek southwest of Ovando. (Photo courtesy of Melanie Trapkus)

Our research clearly shows that harvest, while not affecting population productivity (i.e. maternity), has a dramatic effect on mountain lion survival, and therefore population growth.

uncorrelated with our best independent measures of population sizes and trends, making their utilization detrimental to effective lion management programs and decisions. The measures that were correlated with our best independent measures of population size were imprecise, which in turn meant that their power to detect changes in lion population sizes, and therefore their utility for informing lion management, is limited. Further, some of these techniques, such as track surveys, are very expensive, time consuming, and logistically difficult which also limit their utility for use in lion management.

Logan and Sweanor (2001) described the "sledgehammer approach", where hunting quotas are set mainly by the previous season's hunter success rate. As success rates decline, quotas may be reduced, however due to a lack of inexpensive and reliable methods for tracking populations, even reduced quotas may not match existing population levels, leading to further declines. Our survival modeling suggested that incremental reductions in quotas outside the protected Garnet study area did not result in a significant increase in adult survival until female quotas were reduced to 0.

Our research clearly shows that harvest, while not affecting population productivity (i.e. maternity), has a dramatic effect on mountain lion survival, and therefore population growth. As such, hunting is a very effective tool for managing mountain lion populations. Human harvest is an additive form of mortality that shapes the overall survival structure of mountain lion populations. Adult female mortality > 20% is likely to cause a decrease in population level.

At the same time, we have little power to detect even large changes in population level, or worse yet, belief in indices that actually show no correlation to actual population trends. For these reasons, we recommend further exploration of zone management or metapopulation harvest models. Zone management is thought to reduce the risk of overharvest through preservation of source populations that can sustain hunted areas.

Male kitten M98 at 7 1/2 months of age. (Photo courtesy of Grover Hedrick)

INTRODUCTION - SECTION 1

BACKGROUND

Large carnivores pose a particular challenge in wildlife management. While their potential for conflict with humans is high, their importance in ecosystem function is increasingly well documented (Ray et al. 2005), resulting in often divergent public opinion and management objectives (Riley and Decker 2000). As human populations expand and increase the spatial and temporal overlap between carnivores and humans, there is even greater potential for conflict (Jackson and Nowell 1996, Inskip and Zimmermann 2009). In North America, recent conservation initiatives, as well as changes in prey abundance and distribution have allowed mountain lions (*Puma concolor*), grizzly bears (*Ursus artos*), and wolves (*Canis lupus*) to recover to population levels not seen in decades. Mountain lions in particular have expanded back into ranges from which they were once extirpated (Larue and Nielsen 2008). As these populations continue to increase, public pressure for state officials to monitor and control them is likely to increase as well. Wildlife managers require reliable data and methods in order to make informed decisions that will help mitigate potential and perceived conflicts (Linnell et al. 2001, Treves et al. 2009).

Carnivores are widely hunted for recreation, population control, and to reduce direct and indirect conflict with humans (Packer et al. 2009, Treves 2009). Recreational harvest is used by wildlife managers to provide public opportunity for consumptive, wildlife-related recreation and to control populations for various reasons such as to limit predation impacts on ungulates or to minimize negative public encounters. Modern wildlife management or hunting is premised on the idea of compensatory mortality. Errington (1956) coined the term “doomed surplus” to describe animals that would die by other natural causes if not killed by predators.

Radio-collared adult male M92. (Photo courtesy of Melanie Trapkus)

Today mountain lions occur in all of Montana's ecosystems and ecoregions.

Today many hunting programs assume a similar response to human harvest; namely density dependent compensatory mortality where survival of the remaining individuals in a hunted population is increased through reduced competition. Therefore, how a species responds to harvest is an important management concern. For instance, coyote (*Canis latrans*) control is frustrated by that species' strong compensatory response, where harvest losses are quickly replaced through increased reproduction, survival, and immigration (Knowlton et al. 1999).

Early 20th century eradication programs led to the near extirpation of mountain lion populations by the 1930s. In Montana and western North America populations increased and expanded their range during the 1990s (Cougar Management Guidelines Working Group 2005). Today mountain lions occur in all of Montana's ecosystems and ecoregions (Figure 1.1), their distribution likely tied to vegetative cover type and prey availability (Riley and Malecki 2001).

These elevated mountain lion populations, as well as residential development in lion habitat, have resulted in more interactions between lions and humans (Aune 1991) and the general public has become more aware of the mountain lion presence in Montana. In Montana, public acceptance of mountain lions was found to vary with lion population growth, and perceived risk (Riley and Decker 2000).

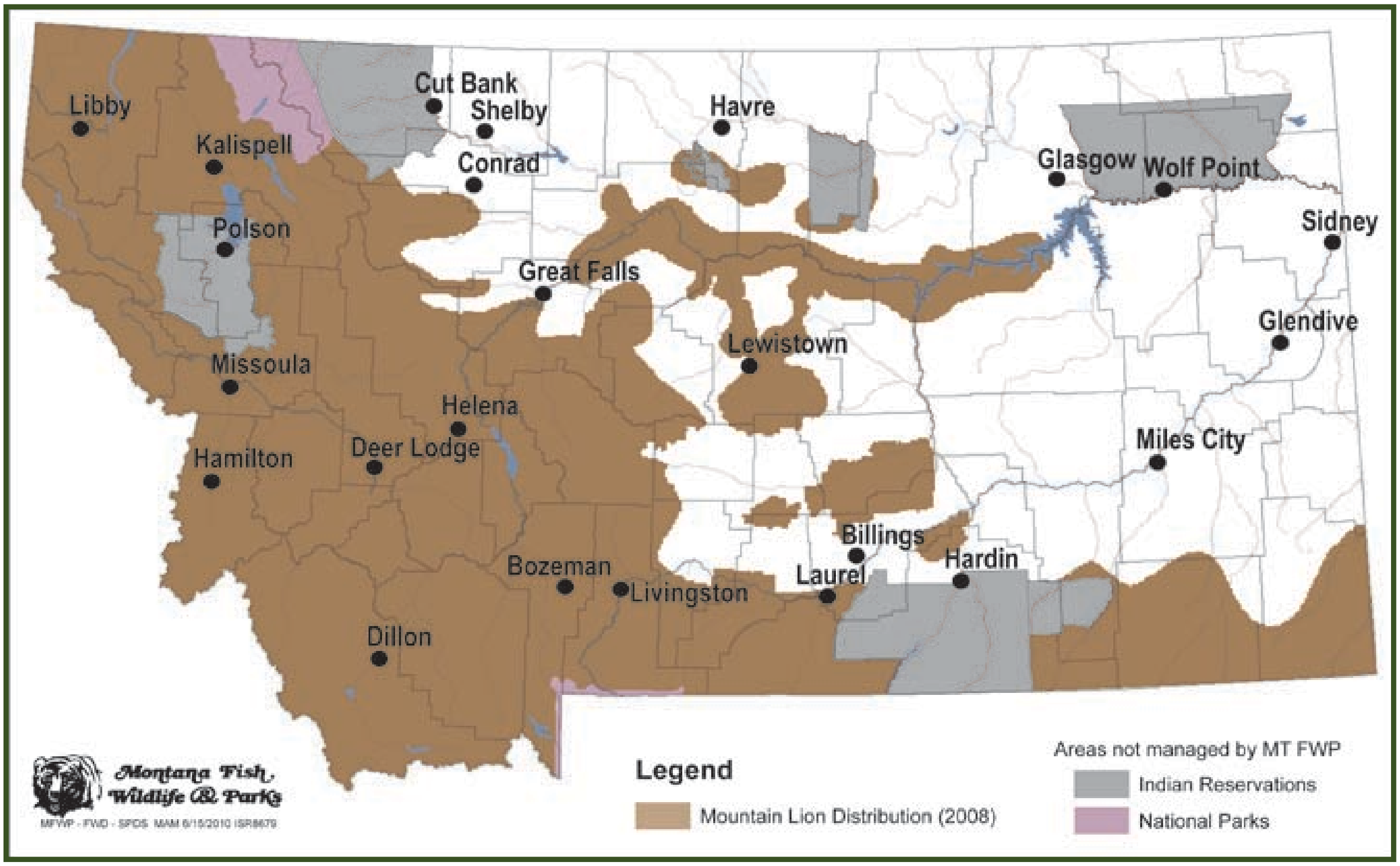


Figure 1.1. Mountain lion distribution in Montana. Distribution is not shown on lands not managed by Montana Fish Wildlife and Parks, although lions are present in both Glacier and Yellowstone National Parks, and may be present on all reservations.

PREVIOUS MOUNTAIN LION RESEARCH IN MONTANA

Prior to this study, mountain lion research had been conducted in Montana near the Fish Creek drainage in the Bitterroot Mountains (Murphy 1983), in the Sun River area of the Rocky Mountain Front (Williams 1992), in Glacier National Park and the North Fork of the Flathead River (Ruth 2004), on the National Bison Range (Choate 2009), and perhaps most extensively in and around Yellowstone National Park (Murphy 1998, Ruth and Buotte 2007). In addition to these telemetry based studies, Riley (1998) conducted an analysis of the human dimensions that affect public perception of mountain lion populations, and the landscape conditions that may contribute to mountain lion distribution across the State.

Beginning in the 1960s, Montana Fish Wildlife and Parks began collecting data on mountain lions by marking them with tags. The first radio-telemetry based study in Montana was conducted by Kerry Murphy as part of his masters research (Murphy 1983). From 1979 to 1982 Murphy radio collared 8 mountain lions in the Fish Creek drainage of western Montana. He concluded that stability was maintained in this hunted population through immigration and recruitment of local juveniles. Hunting pressure was restricted in the drainage due to variations in snow conditions and "agonistic behavior among houndsmen". Recreational harvest therefore appeared to have little influence on lion population dynamics.

During 1991 and 1992 Jim Williams conducted his masters research on a mountain lion population in the Sun River drainage along the eastern front of the Rocky Mountains in northern Montana (Williams 1992). Focusing on habitat and prey selection, he collared 25 animals and found that they selected for forested landcover while avoiding open grasslands and vegetated rock cover. He also found that lions preyed upon both elk and deer at or about their level of availability, while a few animals specialized on bighorn sheep; findings that would be replicated in other study areas in North America (Ross et al. 1997, Cooley et al. 2008). Williams found relatively small home range sizes (male $\bar{x} = 96.4$ km^2 and female $\bar{x} = 58$ km^2)

Prior to this study, mountain lion research had been conducted in Fish Creek, Sun River, Glacier National Park, the National Bison Range and most extensively in and around Yellowstone National Park.

Wildlife biologist Jerry Brown marking a mountain lion in 1976 near Bull Lake south of Troy as part of the first mountain lion research supervised by Ken Greer, Montana's Wildlife Lab Supervisor. *(Photo courtesy of Jerry Brown)*

While all of these studies were conducted on hunted populations none was designed to specifically address the effects of hunting on mountain lion populations.

and considerable home range overlap, although these results may have been biased by a relatively low sample of telemetry locations. There was evidence of intraspecific strife in the population with three documented instances of cannibalism and several animals showing scars presumably from fighting with other mountain lions. Only one study animal was harvested, suggesting that harvest had little influence on the lion population in the study area.

Murphy returned to mountain lion research in 1987 to conduct doctoral research on mountain lions in the northern Yellowstone ecosystem (Murphy 1998). The focus of his research was mountain lion predation and reproductive success. From 1987 to 1996 he collared 80 animals and found that elk and mule deer made up most of the lion's diets. Murphy documented a polygynous breeding system, where males only mated with females within their territory, and females showed strong fidelity to males, breeding with the same male to produce successive litters. Genetic analysis revealed that 4 males sired 78% of sampled litters.

Remains of white-tailed deer killed and cached by subadult male M68. (Photo courtesy of Jeff Sikich)

Toni Ruth was part of a broad study of carnivores, including wolves (Kunkel 1997), coyotes (Arjo 1998), and mountain lions (Ruth 2004), in the north fork of the Flathead River on the border of Montana and British Columbia. This collaborative study focused on the interaction of these three carnivores. From 1993 to 1997 she collared 40 mountain lions, 8 of which were killed by hunters.

David Choate (2009) radio-collared 10 mountain lions on the National Bison Range between 2000 and 2002 as part of his dissertation research into the affect of predation risk on ungulate behavior. Resident mountain lions were thought to be absent from the Bison range between 1970 and 1991. Natural recovery of lions in the area provided a natural experiment on the effects of predation sensitive foraging behavior by deer and elk. One collared mountain lion was killed in a legal hunt when it dispersed off of the National Bison Range.

While all of these studies were conducted on hunted populations none was designed to specifically address the effects of hunting on mountain lion populations. These studies provided excellent information on mountain lion population dynamics, habitat use, home range size, and food habits. However, further research was needed to quantitatively assess the long-term effects of recreational hunting on mountain lion population characteristics.

HUNTING AND MOUNTAIN LION POPULATIONS

Mountain lions were granted game status across much of their North American range during the 1960s, and in Montana mountain lions were classified as game animals in 1971. Since that time, 3 main strategies have been employed by wildlife managers in the harvest of mountain lions: general season (unlimited numbers of either sex may be harvested), limited entry (harvest is limited by restricting the number of licenses sold), and a quota system (harvest is limited by season closure once a prescribed number of animals are taken). A fourth "zone management" (Logan and Sweanor 2001) or "metapopulation" model (Laundre and Clark 2003), has recently been proposed but has seen limited application (e.g. Wyoming Game and Fish Department 2006). Limited entry, quota, and zone management harvest strategies are thought to reduce the risk of overharvest by ensuring a sustainable loss of the total population, reduction of female mortality (limited entry and quota systems), or preservation of source populations that sustain hunted areas (metapopulation model).

Interest in hunting and harvesting mountain lions has remained high over the years - Chris Hedrick holding Queen, Grover Hedrick with Babe and Tim Isaac with harvested adult male lion. *(Photo Courtesy of Grover Hedrick)*

Between 1984 and 1996 a series of papers were published describing the characteristics of mountain lion populations (Hemker et al. 1984, Logan et al. 1986, Ross and Jalkotzy 1992, Lindzey et al. 1994, Spreadbury et al. 1996). While characteristics such as litter size, age of independence, and birth interval did not vary greatly between hunted and non-hunted populations, mortality patterns did. These five studies noted mortality patterns that have been replicated several times since their publication; in hunted populations harvest mortality significantly outweighs all other causes of death, hunted populations have a high level of resiliency, and non-hunted populations may still may have high levels of human caused mortality (i.e. car accidents or poisoning) as well as high levels of intraspecific mortality. Additionally, previous research has shown that some isolated populations have high levels of strife as shown by scaring and other evidence of fighting amongst individuals. This increased natural mortality in non-hunted populations, and evidence of direct competition between individuals, have led some to speculate that hunting may be compensatory (Quigley and Hornocker 2010).

QUANTIFYING MOUNTAIN LION POPULATIONS

Sinclair et al. (2006) state that a wildlife population may be managed in one of four ways:

1. make it increase;
2. make it decrease;
3. harvest it for a continuing yield;
4. leave it alone but keep an eye on it.

Although perhaps over simplified, each of these management actions requires some base knowledge of population trend or level. As a result, a large branch of wildlife research and theory is focused on quantifying populations (e.g. Thompson et al. 1998, Buckland 2001).

In Montana mountain lions were classified as game animals in 1971.

Biologist Bill Semmens holding 5 week old radio-collared female kitten F22. (Photo courtesy of Bob Wiesner)

Because mountain lions are nocturnal, reclusive, mobile, and disperse at low densities, it is difficult to monitor changes in population status and trend. Recent advances have been made in the use of DNA and remote camera mark recapture methods (Beausoleil et al. 2005, Kelly et al. 2008) and research in Utah and Arizona reported positive correlations between track density and mountain lion population (Van Dyke et al. 1986, Van Sickle and Lindzey 1992, Beier and Cunningham 1996). However, to date only extensive radio-collaring programs have provided effective population estimates (Cougar Management Guidelines Working Group 2005).

Public concern over human safety, increased livestock and pet depredation, and predation effects on ungulate populations have been addressed with increased harvest levels.

RESEARCH OBJECTIVES

Despite their acknowledged role in ecosystem function, increases in mountain lion distribution and abundance have resulted in public concern over human safety, increased livestock and pet depredation, and predation effects on ungulate populations. In most jurisdictions in western North America, including Montana, these concerns have been addressed with increased harvest levels. Conversely, due to their importance as a big game species, concern about mountain lion population conservation by consumptive and non-consumptive members of the public, and the recreational and economic benefits associated with mountain lion harvest, sectors of the public have voiced concern over the potential over-harvest of mountain lions. Previous research has shown that mountain lion populations have a high level of resiliency and can recover quickly following cessation of hunting or reduced harvest levels (Lindzey et al. 1992, Logan and Sweanor 2001, Anderson and Lindzey 2005); however some jurisdictions have also seen large oscillations in population levels, likely due to overharvest (e.g. British Columbia and Washington) (Lambert et al. 2006).

In response to public concerns regarding mountain lion populations, Montana Fish, Wildlife and Parks (MFWP) completed an Environmental Impact Statement (EIS) in 1996 which identified the objectives of MFWP's mountain lion management program as:

> "to maintain both mountain lion and prey populations at levels that are compatible with outdoor recreational desires, and that minimize human-lion conflicts and livestock depredation."

In addition, the mountain lion EIS directed MFWP to update and refine its statewide management strategy by:

> "determining the carrying capacities of different habitats within the state for mountain lions and their prey; improving its ability to monitor populations and determine their status, composition and trend; improving the regulation of the annual harvest; improve the public understanding of mountain lion biology, habitat requirements and management; and developing policies and a proactive program to deal with

human-lion confrontations and livestock depredation".

Consistent with this strategy and the information needs relative to mountain lion conservation in Montana, our research objectives were to:

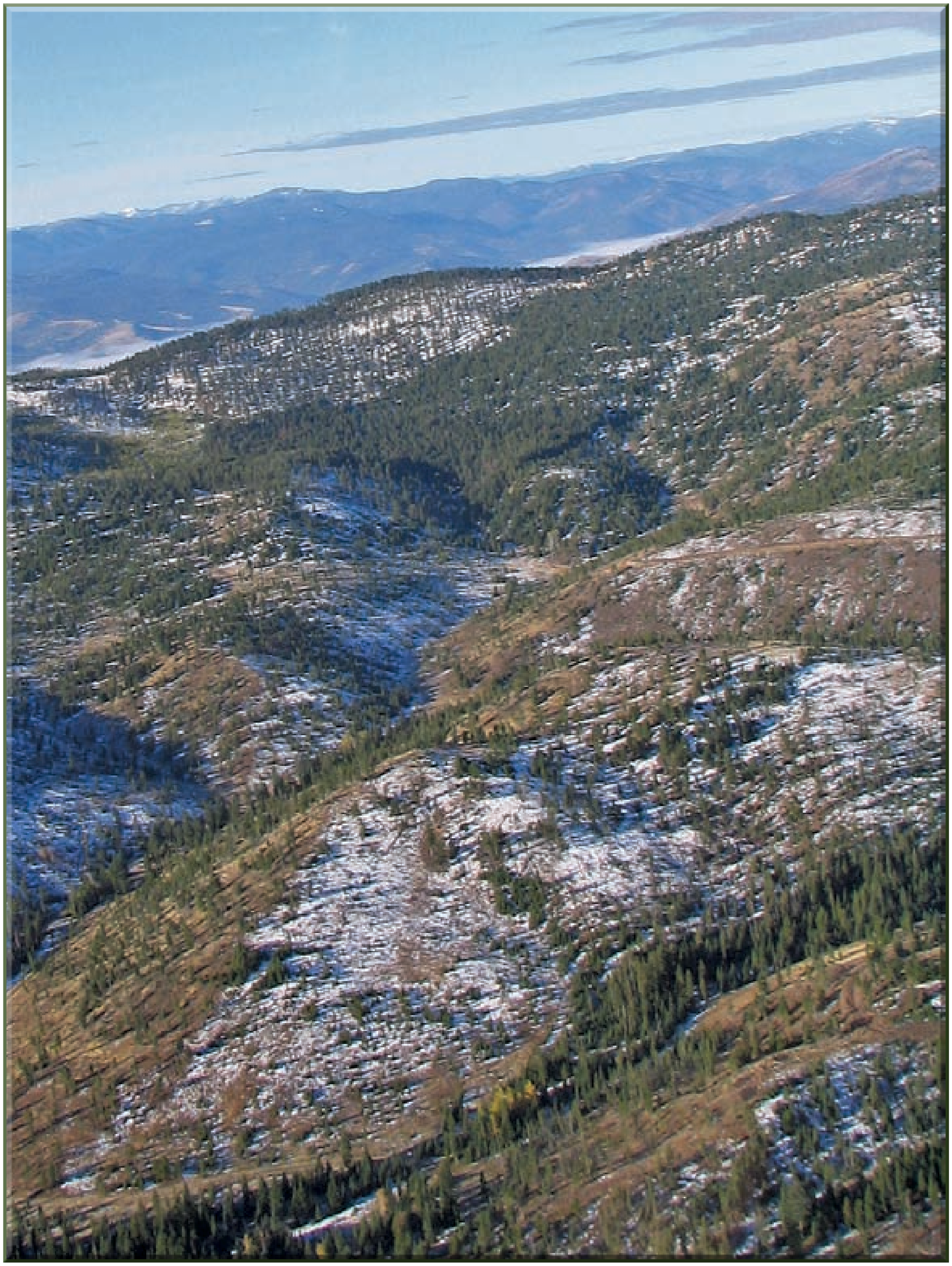
1. Document population characteristics of a hunted mountain lion population in the mountain/foothill habitat type including density, composition, productivity, mortality, recruitment, dispersal and home range size.
2. Evaluate the accuracy of track surveys and other management applicable techniques to detect trend in mountain lion abundance.

REPORT FORMAT

We provide a description of the study area and general study methods in Section 2. In Section 3 we provide descriptive statistics of basic population parameters including those thought to be altered by harvest and density (i.e. home range overlap, maternity, population structure, etc.). In Section 4 we examine survival and mortality differences in hunted and non-hunted populations and examine evidence of the compensatory or additive nature of hunting mortality. In Section 5 we model population growth within the watershed, and in Section 6 we compare various commonly collected population indices to our modeled population levels. Finally in Section 7 we discuss the management implications of this research and provide recommendations on future research needs.

Our research objectives were to document population characteristics of a hunted mountain lion population and to evaluate the accuracy of track surveys and other techniques to detect trend in mountain lion abundance.

Blackfoot River at the junction with the North Fork of the Blackfoot, south of Ovando. *(Photo courtesy of Melanie Trapkus)*



The southern portion of Garnet Mountains at the top of the West Fork of Cramer Creek looking west toward mouth of Rock Creek. (Photo courtesy of Melanie Trapkus)

STUDY AREA AND GENERAL METHODS - SECTION 2

STUDY AREA

The study was conducted in the Blackfoot river watershed (7,908 km²) in Powell, Granite, Lewis and Clark, and Missoula counties in west-central Montana (Figure 2.1). The area is characterized by relatively moderate rolling topography, with gentle to moderate slopes dissected by steep limestone canyon areas along drainages (Brainerd 1985). This area is representative of much of western Montana, a mountainous mix of private (i.e. Plum Creek Timber Company and private land owners) and public lands (i.e. Bureau of Land Management, Helena and Lolo National Forests) with elevations ranging from 1,160 m to 2,156 m (Montana Fish, Wildlife & Parks 2004). Mean temperatures range from -8.9° C in January to 18.9° C in July with mean annual precipitation ranging from 19-33 cm occurring primarily from December to June (Western Regional Climate Center, Ovando, MT).

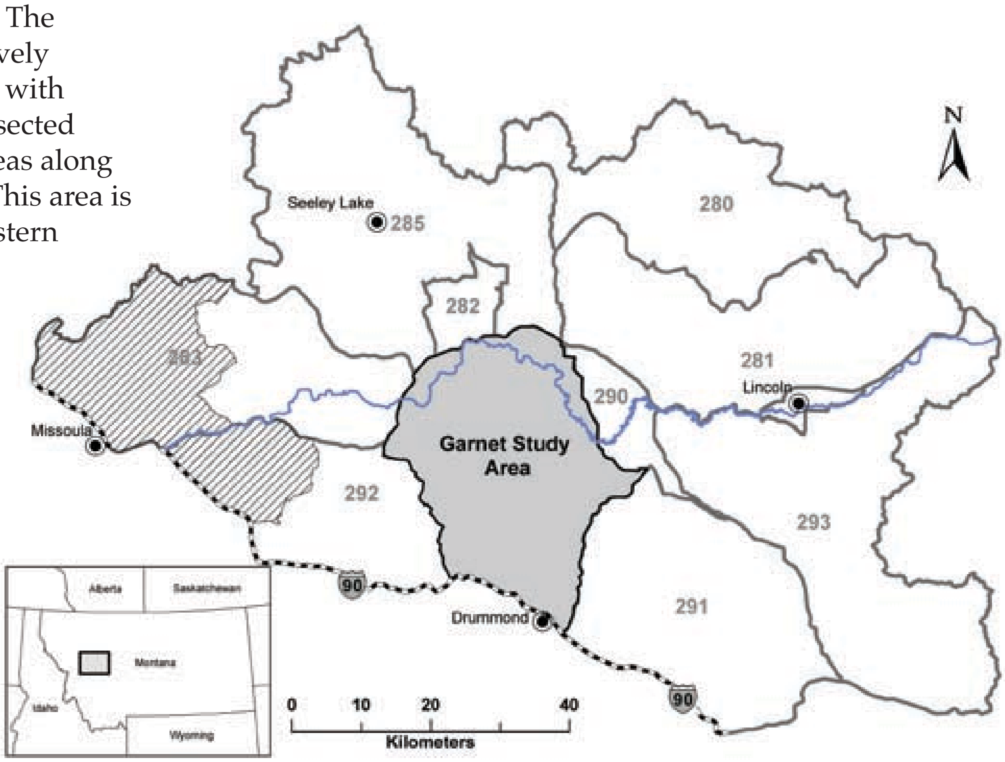


Figure 2.1 The Garnet study area (915 km²), and greater Blackfoot river watershed (7908 km²) western Montana. Crosshatching represents a portion of the Missoula Special Management Unit, numbers represent Montana Fish, Wildlife and Parks hunting districts. See Study Design for explanation regarding varying mountain lion harvest levels in each jurisdiction.

Mountain lions were radio-collared through intensive capture efforts during winters (November to March) 1997-2007.

Dominant land cover varies from high elevation mixed lodgepole pine (*Pinus contorta*)-subalpine fir (*Abies lasiocarpa*) stands, to more mesic Douglas-fir (*Pseudotsuga menziesii*)-western larch (*Larix occidentalis*) stands at mid-elevations, and Douglas fir, ponderosa pine (*Pinus ponderosa*), and aspen (*Populus tremuloides*) at low elevations. Valley bottoms consist of a mixture of irrigated and dry land agriculture, and native bunchgrass-sagebrush (*Artemisia* spp.)-juniper (*Juniperus scopulorum*) communities (Lehmkuhl 1981). The majority of the low to mid-elevation forests have been logged in the past 50 years (Raithel 2005).

Ungulate prey species present in the area include elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*) and moose (*Alces alces*). Large predators besides mountain lions include black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*). Smaller predators include bobcat (*Lynx rufus*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), pine marten (*Martes americana*) and long-tailed weasel (*Mustela frenata*). Wolf (*Canis lupus*) presence during the study period was negligible, with the first confirmed pack (Elevation Mountain) established in 2006, the last year of our study (Montana Fish, Wildlife and Parks 2006).

CAPTURE AND MONITORING

Mountain lions were radio-collared through intensive capture efforts during winters (November to March) 1997-2007. We used trained hounds to tree lions when fresh tracks were located in the snow. Treed lions were darted and drugged with a mixture of ketamine hydrochloride and xylazine delivered using a Pneu-Dart Model 193SS cartridge fired rifle with disposable darts (Pneu-Dart Inc. P.O. Box 1415, Williamsport, PA 17703). Once the drug had taken effect, a member of the crew would climb to the lion and secure its back legs with a rope and lower it to the ground. The lions were given the antagonist Yohimbine to counteract the Xylazine before release.

Captured lions were given an estimated age by tooth replacement or wear (Ashman et al. 1983) and placed into 1 of 3 age categories: adult (>24 months), juvenile (13-24 months) and kitten (0-12 months). One of 3 sizes of Teloncis (Telonics 932 E. Impala Ave., Mesa, AZ 85204-6699) collars were used depending on the size/age of the cat: an expandable (20cm – 34cm) kitten collar equipped with a Mod-073 transmitter, a juvenile collar equipped with a Mod-305 transmitter, or an

Tooth wear, replacement, and color were used in aging lions - male kitten M25 at 8 months of age. (Photo courtesy of Bob Wiesner) adult collar equipped with a Mod-500 transmitter. Lions were located from the air approximately twice per week. Beginning in 2001, GPS collars programmed to acquire a location every 5 hours were fitted to newly collared animals and replaced VHF collars on already marked animals as opportunity allowed.

When a female became localized for a short period of time, we investigated the site to determine if she had given birth. Kittens were collared (without drugging) approximately 1 month from the time the mother had localized. Expandable Mod-073 collars remained on kittens up to 7 months of age; mod-305 collars remained on juveniles up to 10 months of age. A mod-500 adult collar was put on through adulthood. As radioed lions approached the size limit of a collar size, they were captured and fitted with another collar of the appropriate size.

A total of 121 individual mountain lions were captured between January 1998 and December 2006 (Table 2.1), a total of 152 times, including 82 kittens, and 39 juveniles and adults >12 months of age. Of these, 117 individuals were collared and monitored for habitat use and survival. On average animals were monitored for 502 days (approximately 16 months) with a range of 7 to 3231 days with males remaining on the air for shorter periods (284 days) than females (658 days) (Figure 2.2 and Figure 2.3). Known fates were recorded for 65 animals, with the remainder being right-censored. They were used in analysis until their loss due to collar failure, their dispersal from the study area, or survival to the end of the study.

Radio-collared male kitten M23 at 5 weeks old. (Photo courtesy of Milo Burcham)

As radioed lions approached the size limit of a collar size, they were captured and fitted with another collar of the appropriate size.

Table 2.1. Sex and age of mountain lions captured in the Blackfoot drainage, Montana, 1998-2006.

	Age at capture (months)	1998	1999	2000	2001	2002	2003	2004	2005	2006	Total
Females	<12	10		5	5	3	5	6	7	3	44
	13-24	3		1		1		2			7
	25-36	1		3	1			1			6
	36+	5	3	1	1	2	1		1		14
Males	<12	7	2	1	3	5	2	3	11	4	38
	13-24							1			1
	25-36	2			1			1		1	5
	36+			1	1	1	1	1	1		6
Total		28	5	12	12	12	9	15	20	8	121

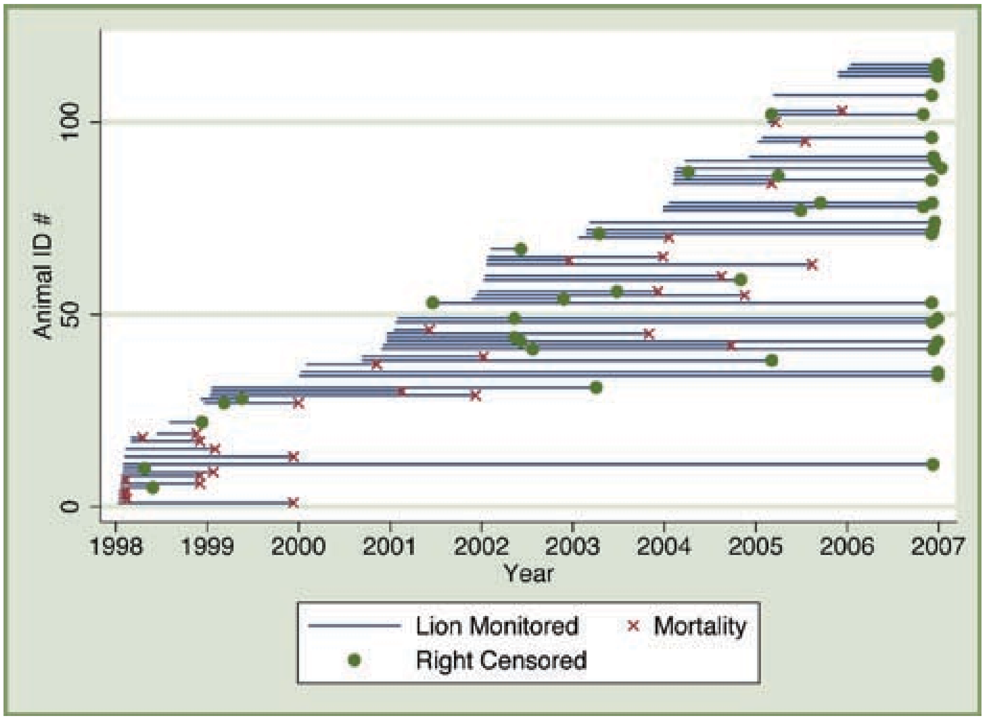


Figure 2.2 Encounter record for radio-collared female mountain lions in the Blackfoot river drainage, Montana (1998-2007). Red Xs denote mortality, while green circles denote animals that were right censored (i.e. dropped their collars, left the study area, or survived to the end of the study).

Original photo - uncollared female lion. (Photo courtesy of Bob Wiesner)

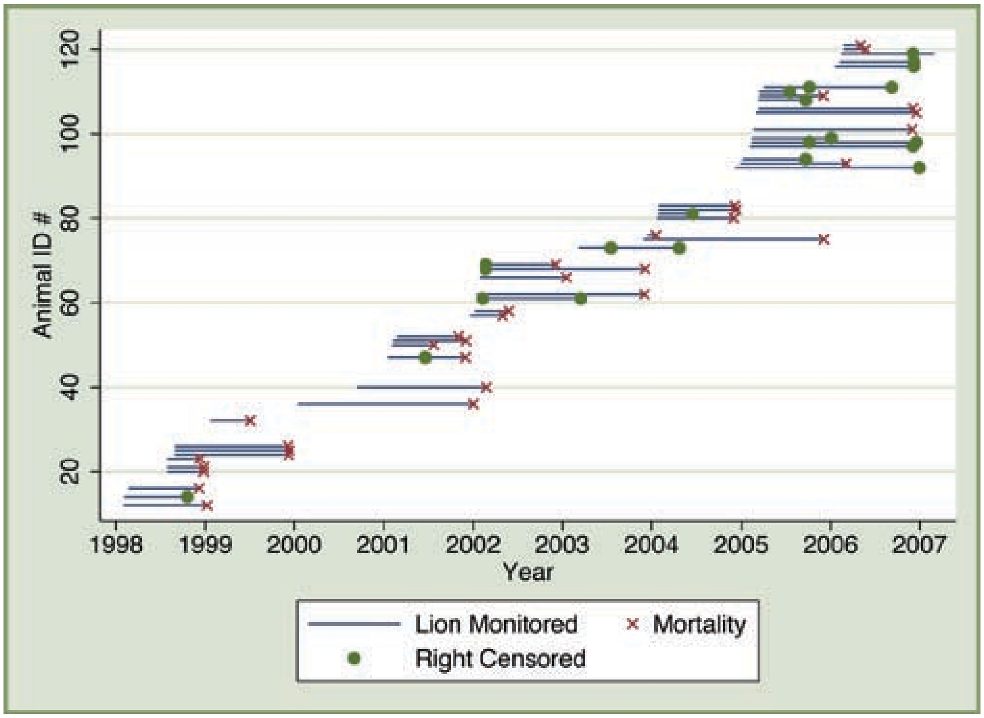


Figure 2.3 Encounter record for radio-collared male mountain lions in the Blackfoot river drainage, Montana (1998-2007). Red Xs denote mortality, while green circles denote animals that were right censored (i.e. dropped their collars, left the study area, or survived to the end of the study).

STUDY DESIGN

Research was focused within Montana's hunting district 292, although mountain lions were also radio-collared and monitored in the surrounding districts of the Blackfoot river watershed (Figure 2.1). We investigated population effects of harvest on mountain lions using a pseudo-experimental before-after-control-impact (BACI) design. In December 2000, following three years of hunting, approximately two-thirds of district 292 was closed to mountain lion hunting effectively creating a refuge (hereafter referred to as the Garnet study area), representing approximately 12% (915 km^2) of the greater Blackfoot watershed (7,908 km^2). Hunting continued in the remainder of the drainage, but harvest levels declined between 2001 and 2006 as quotas were reduced (Table 2.2). The Missoula special management area (MSMA), is a 1929 km^2 area surrounding the city of Missoula designed to reduce mountain lion densities and possibly lion/human conflicts through high levels of harvest. A portion of the MSMA (680 km^2) overlapped the Blackfoot watershed (Figure 2.1). Quotas in the Missoula special management area were 25 total lions between 1998 and 2004, then reduced to 20 for the final 2 years of the study. We used this experimental design to examine the effects of human harvest on this mountain lion population.

A major focus of our research was to better understand how hunter harvest was affecting mountain lion survival. (Photo courtesy of Grover Hedrick)

We used this experimental design to examine the effects of human harvest on this mountain lion population.

STATISTICAL ANALYSIS

Unless otherwise noted, all statistical analyses were conducted using Stata 11 (Stata Corp, College Station, TX, USA).

Table 2.2. Mountain lion harvest quotas for Blackfoot river watershed Montana, 1998 to 2006. Beginning in December 2000 the study area was managed separately from the remainder of the Blackfoot watershed (see also Figure 2.1).

	Sex	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Garnet managed as part of Blackfoot watershed.			0	0	0	1*	0	0
	Male				0	0	0	1*	1	1
Blackfoot Drainage (excluding MSMA)	Female	30	41	30	15	9	3	3	0	0
	Male	40	33	29	21	9	7	7	7	7
Missoula Special Area Mgmt. (MSMA)	Female	15	15	15	15	15	15	15	10	10
	Male	10	10	10	10	10	10	10	10	10

* One either sex permit issued in 2004.

Houndsmen Grover Hedrick, Tony Knuchel and Sanford Strout with hounds Sugar, Stash and Cooter treeing adult male M92. (Photo courtesy of Melanie Trapkus)

POPULATION CHARACTERISTICS OF A HUNTED MOUNTAIN LION POPULATION - SECTION 3

INTRODUCTION

The earliest research on mountain lion populations in the Idaho primitive area suggested a self regulatory system of population control; the land tenure system (Hornocker 1969). The land tenure system is premised on social behavior as limiting population level through territoriality and its effects on recruitment, natality, and mortality (Seidensticker et al. 1973). Hornocker surmised that the land tenure system was adaptive, and negated the possibility that prey populations would be depleted due to the spatial limitations of territorial animals. Territoriality is thought to limit the numerical response of predators, causing the population to asymptote below a density set purely by prey availability (Solomon 1949).

The idea that mountain lion populations are limited by social interaction has been challenged over the past decade. Hornocker's (1969) original work suggested that home ranges were "inviolate". Recent work however suggests that home range overlap may vary greatly in hunted populations (Maletzke 2010), leading to a paradoxical effect of increased density in hunted populations. Mountain lions are also known to migrate seasonally to follow prey. Seidensticker et al. (1973) found that the density of mountain lions in their study area almost doubled during winter in response to migrating deer and elk populations. By radio collaring both predator

The earliest research on mountain lion populations in the Idaho primitive area suggested a self regulatory system of population control; the land tenure system.

Radio-collared adult female F49. *(Photo courtesy of Tonya Chilton)*

Harvest may disrupt the social structure of males and their ability to define and defend exclusive home ranges.

Females, whose reproductive success is maximized by rearing young to dispersal, delineate their home ranges based on prey availability.

and prey, Pierce et al. (2000) concluded that mountain lion distributions on a winter range in California were the consequence of prey availability, and not land tenure or mutual avoidance. Logan and Sweanor (2001) proposed a "two-strategies," or reproductive strategy, hypothesis whereby each sex would employ a social organization system that maximized their specific reproductive success. Females, whose reproductive success is maximized by rearing young to dispersal, delineate their home ranges based on prey availability. Conversely males, whose reproductive success is maximized by the number of breeding opportunities they can secure, maintain exclusive home ranges based on female availability. The reproductive strategies hypothesis was recently supported by research in Washington State. Maletzke (2010) compared heavily and lightly hunted populations of mountain lions and found larger male home ranges with greater overlap in the heavily hunted population with no difference in female home range characteristics. This suggests that harvest may disrupt the social structure of males and their ability to define and defend exclusive home ranges.

Radio-collared adult female F11 showing evidence of nursing. She produced 6 litters of kittens during 9 years of monitoring. (Photo courtesy of Brian Shinn)

The reproductive strategies hypothesis is based on the concept of fitness, where fitness is defined as "the relative reproductive success of an individual in the long term" (Sinclair et al. 2006). Here the phrase "long term" means several generations, and therefore reproductive success does not simply include maternity (the number of kittens born per female per year), but rather the survival and successive reproduction of offspring and all that contributes to that survival. In this light, hunting may affect fitness, and ultimately population levels in a number of ways. Hunting clearly affects individual survival directly; however how, or if, these disruptions on individuals affect the greater population is less clear. Hunting may affect population sex and age structure, maternity, dispersal and recruitment patterns, as well as home range size and overlap.

Mountain lions, like many carnivore species, display high levels of juvenile dispersal (Chepko-Sade et al. 1987, Zimmermann et al. 2005). While males disperse to avoid inbreeding regardless of population density (intrinsic dispersal), females disperse to avoid intraspecific-competition (Greenwood 1980, Logan and Sweanor 2001). Sweanor et al. (2000), in an non-hunted population, found that 68% of female recruits came from the local population, while an equal or slightly greater proportion of male recruits were immigrants. Human harvest may reduce intraspecific competition for females thus lowering dispersal rates when compared to non-hunted populations. Hunting may also create home range vacancies for males, which given an accessible source population, are quickly filled by juveniles (Robinson et al. 2008).

The effect of these dispersal patterns may cascade through a hunted population affecting other population parameters and therefore scaling into greater population level effects. For instance, hunting has been shown to skew the sex and age ratio of a population towards younger males (Robinson et al. 2008). Logan and Sweanor (2001) hypothesized that loss of dominant, territorial males may increase instances of infanticide; the killing of unrelated offspring. Evidence of infanticide, and conversely the stabilizing effect of territorial males, has been found in a variety of mammals as diverse as rodents, baboons and grizzly bears (Bellemain et al. 2006, Boyko and Marshall 2009, Fernandez-Gil et al. 2010, Moscovice et al. 2010) (see Section 4 for further discussion.) Kitten production (maternity) may also be lowered in hunted populations if younger males do not breed successfully, or if female recruitment is restricted and maternity is reduced in the remaining higher aged females.

In this chapter we provide a descriptive overview of population characteristics that may be altered by human harvest. We hypothesized that hunting would reduce emigration while increasing philopatry. Based on the "two-strategies" hypothesis we predicted that female home range size would be smaller in the heavily hunted population due to increased prey availability, while male home range and overlap would be larger in the hunted population due to reduced intraspecific competition with other males. Maternity of individuals should be enhanced by hunting, due to reduced competition for resources (Sinclair et al. 2006). Survival, cause-specific mortality, and population growth are treated in Sections 4 and 5.

METHODS

Sex and Age Structure

We established a minimum population estimate for the Garnet study area each year of the study by back-calculating the lifespan of all mountain lions known to have been present in the study area including collared and harvested animals (Logan and Sweanor 2001, Stoner et al. 2006, Robinson et al. 2008). Our estimate was based on the number of animals, in all age classes, thought to be present on December 1st (the beginning of the hound hunting season) of each year. Based on the degree of relatedness determined

We hypothesized that hunting would reduce emigration while increasing philopatry.

Biologists Doug Powell and Melanie Trapkus fitting adult female F88 with a GPS collar. (Photo courtesy of Melanie Trapkus) from DNA analysis (unpublished data), we assumed that all males were immigrants, while all females were recruited from within the population. Therefore males were backdated to 2 year old (immigrating into the population after their second birthday), while females were backdated to 1 year old. We assumed females were philopatric and were likely born inside the Blackfoot watershed, however we could not be sure if they were born inside or outside the Garnet study area. We used a z-test to compare the mean ages of adults, and proportion of the population consisting of adults between the hunted and non-hunted populations (Zar 1999).

We tested the hypothesis that litter size would increase in a hunted population due to increased available resources using a repeated measures analysis of variance.

Reproduction

Estimates of litter size can be biased low if den sites are not investigated early enough that true litter size is known and no kittens have already died (Ross and Jalkotzy 1992). Because of this potential bias, we estimated average litter size in two ways, first based on litter size when kittens were observed at den sites, which assumes no bias as litters are observed early enough that little or no kitten mortality has occurred, and second using all encountered litters regardless of their estimated age when first encountered which may be biased low due to undetected kitten mortality. We tested the hypothesis that litter size would increase in a hunted population due to increased available resources using a repeated measures analysis of variance (ANOVA) to compare litter size within the Garnet study area during hunting and non-hunting periods (Zar 1999).

By radio collaring kittens and juveniles still traveling with their mothers, we were able to observe both age at dispersal and, for animals that did not leave the study area, first reproduction. We were also interested in how or if female age affects fertility or litter size. Using a repeated measures analysis of variance (ANOVA) we tested for an age effect on litter size in the female mountain lions we monitored (Zar 1999). Paternity was based on DNA analysis.

Related to litter size is the commonly reported measure of maternity. Maternity rate is defined as the mean number of young born per reproductive female per year (Caswell 2001). Some researchers have used litter size, mean birth interval, and proportion of females traveling with young as a surrogate measure of maternity (e.g.Lambert et al. 2006), however this may introduce a bias by excluding females that fail to reproduce. We estimated maternity rate based on the total number of kittens born to all radio-collared females of reproductive age (>24 months) monitored within the

Ten day old kittens of female F42. (Photo courtesy of Brian Shinn)

Garnet study area. We tested for a hunting effect on maternity rate using a z-test (Zar 1999).

Dispersal

Dispersal was defined as a juvenile establishing a home range with < 5% overlap of their maternal home range, while juveniles establishing home ranges with > 5% overlap were considered to be philopatric (Logan and Sweanor 2001). Dispersal rate was based on the number of independent juveniles in each year that moved outside their maternal home range compared to the number monitored.

Home Range

Home range estimation is sensitive to sample size, method, and in the case of kernel estimators, smoothing factor (Silverman 1986, Seaman et al. 1999). Sample size requirements for proper estimation are acquired by determining the point at which home range size asymptotes (Swihart and Slade 1985). For mountain lions, home range size has been shown to asymptote at 26 weeks and 37 locations (Logan and Sweanor 2001, Knopff 2010).

Southern portion of Garnet Mountains at the upper end of Deep Creek looking south toward Bearmouth. (Photo courtesy of Melanie Trapkus)

We constructed annual 95% volume fixed kernel home ranges in ArcGIS using program HRT: Home Range Tools (Rogers et al. 2005) for independent mountain lions with a minimum of 26 weeks of data and 37 locations in each year. Kernel methods of home range estimation use a smoothing parameter or bandwidth (*h*) to estimate the degree of uncertainty or spread around each location. The adaptive kernel method selects a local bandwidth for each observation while the fixed method uses the same bandwidth across the entire home range. A low value of *h* gives the estimate a small value of spread around each point and a more variable (undersmoothed) home range, while a high value of *h* has the opposite effect. HRT calculates a reference smoothing factor (h_{ref}) as the square root of the x and y coordinate mean variances divided by the sixth root of the number of points used (Worton 1995, Rogers et al. 2005). Several methods have been proposed to calculate an optimal smoothing factor. The use of the h_{ref} value can oversmooth multimodal data resulting in larger home-range areas than other methods (Silverman 1986), which has lead to the popular use of the least squares cross validation (LSCV*h*) method for selecting *h*. However LSCV can oversmooth and create a highly fragmented home-range estimate especially when sample sizes are small, very large, or when several locations are at or near the same point

Home range estimation is sensitive to sample size, method, and in the case of kernel estimators, smoothing factor.

(Kernohan et al. 2001, Horne and Garton 2006). Because our study was a combination of long interval (weekly) VHF and short-interval (5hr) GPS locations with a relatively high degree of accuracy (D'eon et al. 2002) no single objective method of finding an optimal smoothing factor fit our desire to use a single method for all data. We therefore selected a smoothing parameter of 1.0 x h_{ref}. Although this is a subjective selection of smoothing parameter (Silverman 1986) it is based on the objective method of h_{ref} and is therefore replicable by other studies using similar data sets. Because we were interested in home range overlap, we chose fixed kernels over adaptive due to their lower bias, especially at the outer contours (Seaman et al. 1999).

Our minimum population estimate for the Garnet study area ranged from 37 lions in 1997 to a low of 20 in 1999, before recovering to 33 in 2006.

We calculated a two dimensional measure of overlap between contiguous home ranges of each sex, in each year. We used Hawth's tools "polygon in polygon" function for ArcGIS 9.3 to calculate the total shared area between home range polygons. We calculated percent overlap for each animal by dividing the area of overlap by that animal's annual home range. We conducted a repeated measures analysis of variance (ANOVA) on percent overlap to test the hypothesis that home ranges and overlap would be larger in the hunted population due to reduced intraspecific competition.

RESULTS

Sex and Age Structure

Our minimum population estimate for the Garnet study area ranged from 37 lions ($4.0/100km^2$) in 1997 to a low of 20 ($2.2/100km^2$) in 1999, before recovering to 33 ($3.6/100\ km^2$) in 2006 (Figure 3.1). The average age of adult females increased from 3.53 years during the hunted period to 4.83 in the non-hunted population although this difference was not significant ($Z = -1.47$, $P = 0.14$). Similarly the average age of adult males increased from 2.73 to 3.52, however this increase was also non-significant ($Z = -1.46$, $P = 0.14$). The oldest radio-collared female monitored during the study was 10 years old, the oldest male was 6.

Over the course of the study the population was on average made up of 37% adult females, 15 % adult males, 17% juveniles, and 30% kittens. While the proportion of adult females in the population remained relatively constant between the hunted and non-hunted phases ($Z = 1.20$, $P = 0.22$), the proportion of adult males in the non-hunted population declined significantly from 21% to 10% ($Z = 2.87$, $P < 0.01$) (Figure 3.2).

Reproduction

Mean total litter size, when dens were visited early enough to observe all kittens, was 2.92 ($n = 24$, 95% CI 2.70 – 3.13), while our estimate of litter size, not accounting for kittens missed at the den was 2.33 ($n = 39$, 95% CI 2.04 – 2.62). Neither estimate of litter size

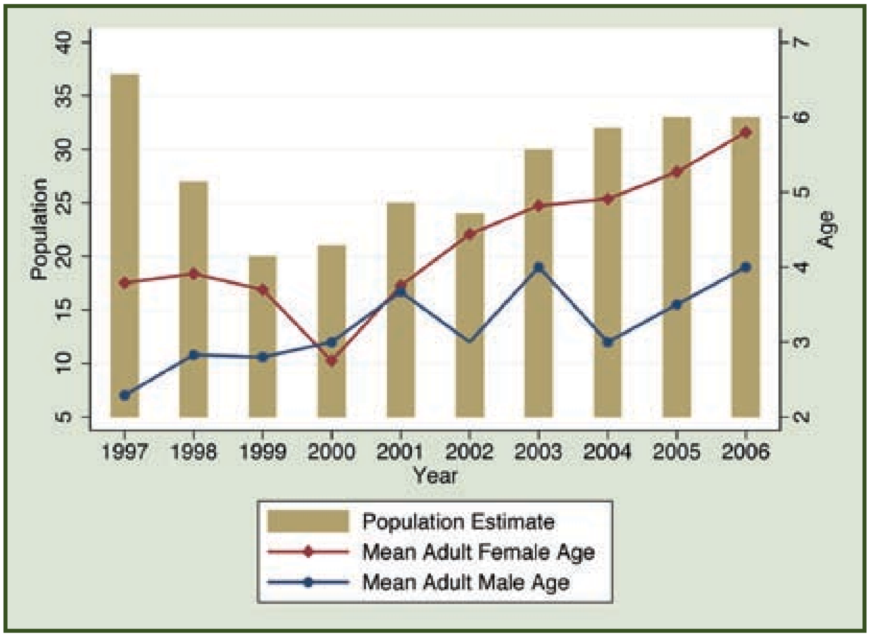


Figure 3.1 Minimum mountain lion population estimate, and mean adult age censused on December 1st, 1997 - 2006, Garnet study area, western Montana.

was affected by hunting (*F* = 0.27, df= 1, *P* = 0.61 and *F* = 0.60, df= 1, P = 0.45 respectively). Of 32 litters where birth month could be confirmed, mountain lions gave birth in all months but December, February and March with most litters born during the period from July to October (Figure 3.3). Fourteen known aged females gave birth to their first litter at a mean age of 31.4 months (Range 23-37 months). We found no effect of female age on litter size (*F* = 0.22, df = 6, P = 0.96). Average birth interval was 602.6 days (95% CI 503 – 702) or 19.8 months. On average approximately 58% of females 24 months or older gave birth each year, while 89% of females were travelling with dependent young.

Paternity was determined for 20 of the 47 litters encountered during the study. The mean age of sires was 35 months (Range 15 to 57 months). The youngest male sire was M47 who was 15 months old when he first bred, and went on to sire 4 more litters with 3 other females.

The mean maternity rate across the study period was 1.29 (95% CI 0.84 – 1.76) kittens per female per year. Although maternity was lower during the hunting period ($\bar{x}$=1.08, 95% CI 0 – 3.59) as compared to the protected population ($\bar{x}$=1.40, 95% CI 1.02 – 1.78) this difference was not significant (Z = -0.53, P = 0.59).

Dispersal

From 1998 to 2006 we monitored 66 mountain lions (39 female and 27 male) during their juvenile year (13 to 24 months of age). Of these 66 individuals 47 survived to independence. Average age at dispersal was 15 months, and ranged from 11 to 23 months. Dispersal was severely constrained in the hunted population prior to 2001. During the first three years of study when hunting pressure was high, although

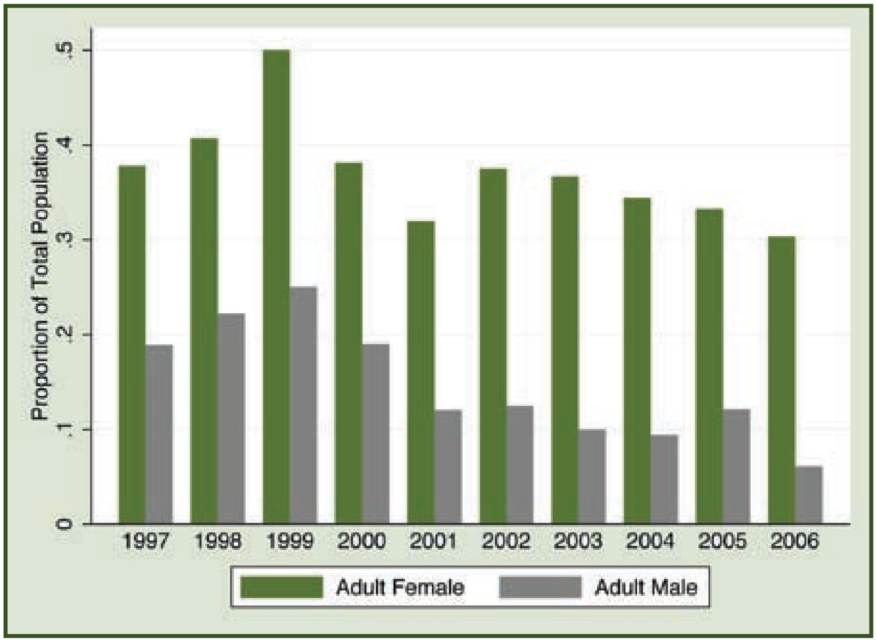


Figure 3.2. Proportion of minimum population estimate consisting of adult male and female mountain lions December 1st 1997 – 2006, Garnet study area, western Montana.

On average approximately 58% of females 24 months or older gave birth each year, while 89% of females were travelling with dependent young.

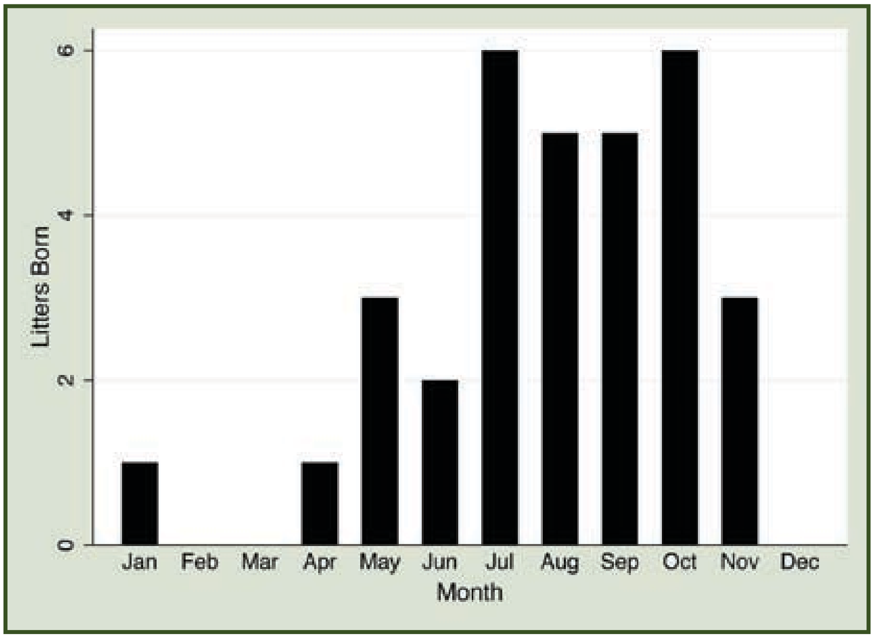


Figure 3.3. Number of mountain lion litters born during each month, Garnet study area 1998 – 2006.

12 juvenile lions were monitored, only 2 females survived to independence. One dispersed out of the Blackfoot drainage, and one established a philopatric home range inside the Garnet study area. Between 2001 and 2006, during protection of the Garnet from hunting, we monitored 54 juvenile mountain lions, 45 of which survived to independence. In total, over the course of the study, female juveniles showed equal levels (50%) of dispersal and philopatric behavior. We did not document any philopatric behavior in radio-collared juvenile males (i.e. 100% dispersal).

We did not document any philopatric behavior in radio-collared juvenile males (i.e. 100% dispersal).

Home Range Size and Overlap

Within the Garnet study area, we collected sufficient data to estimate 63 annual home ranges for 27 females, and 9 annual home ranges for 7 males. Mean annual female fixed kernel home range size in the Garnet study area was 275 km^2 (SE = 25) with 33% overlap with adjacent females (SE = 0.02) (Figure 3.4). Mean annual male fixed kernel home range size in the Garnet study area was 687 km^2 (SE = 120) with 22% overlap with adjacent males (SE = 0.08) (Figure 3.5). Counter to our hypothesis of increased prey availability in the hunted population, mean home range size was

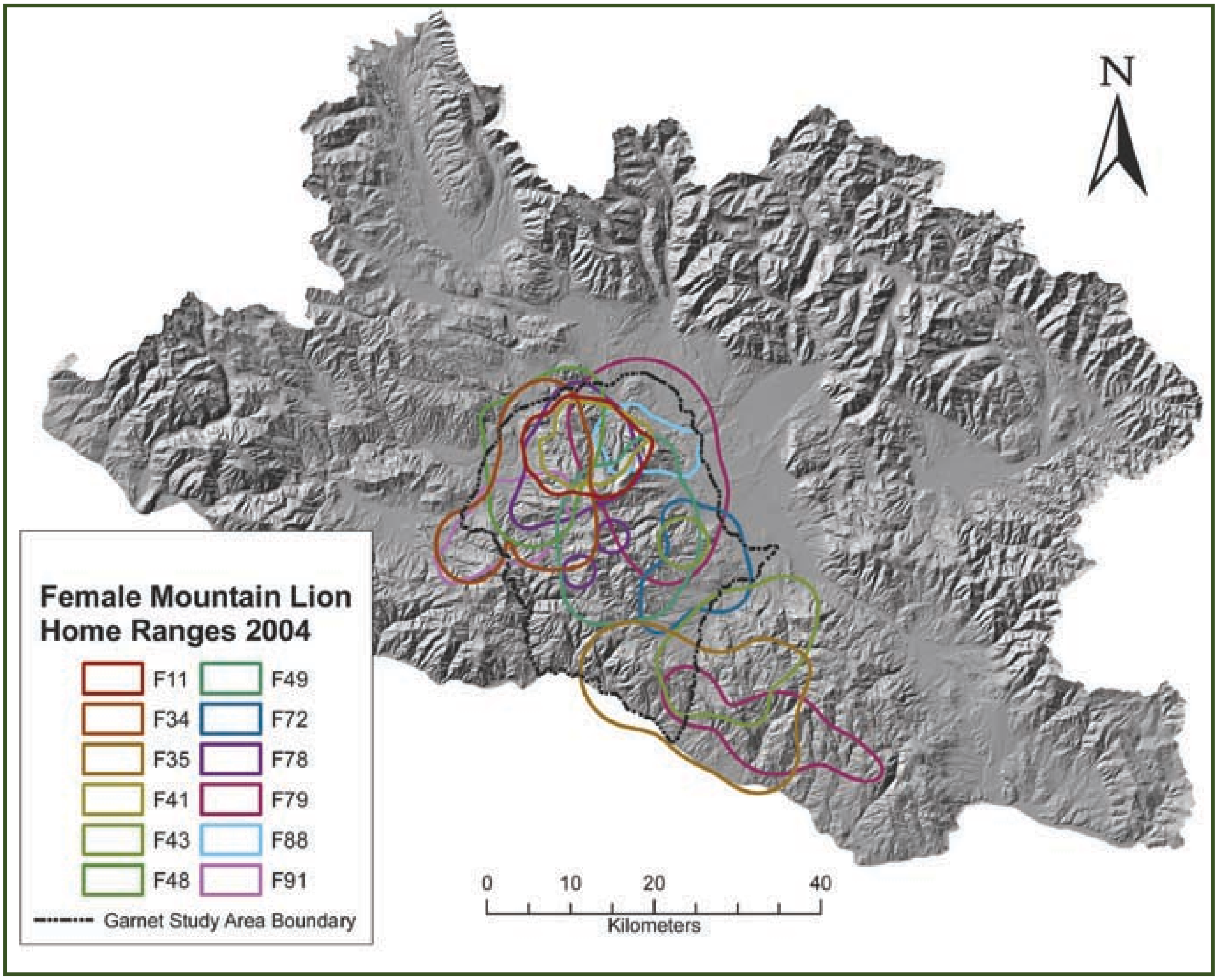


Figure 3.4 Female annual 95% fixed kernel home ranges in 2004. The year 2004 is displayed as an example of home range size and overlap as it was in this year when the greatest number of independent animals were monitored inside the Garnet study area, Montana.

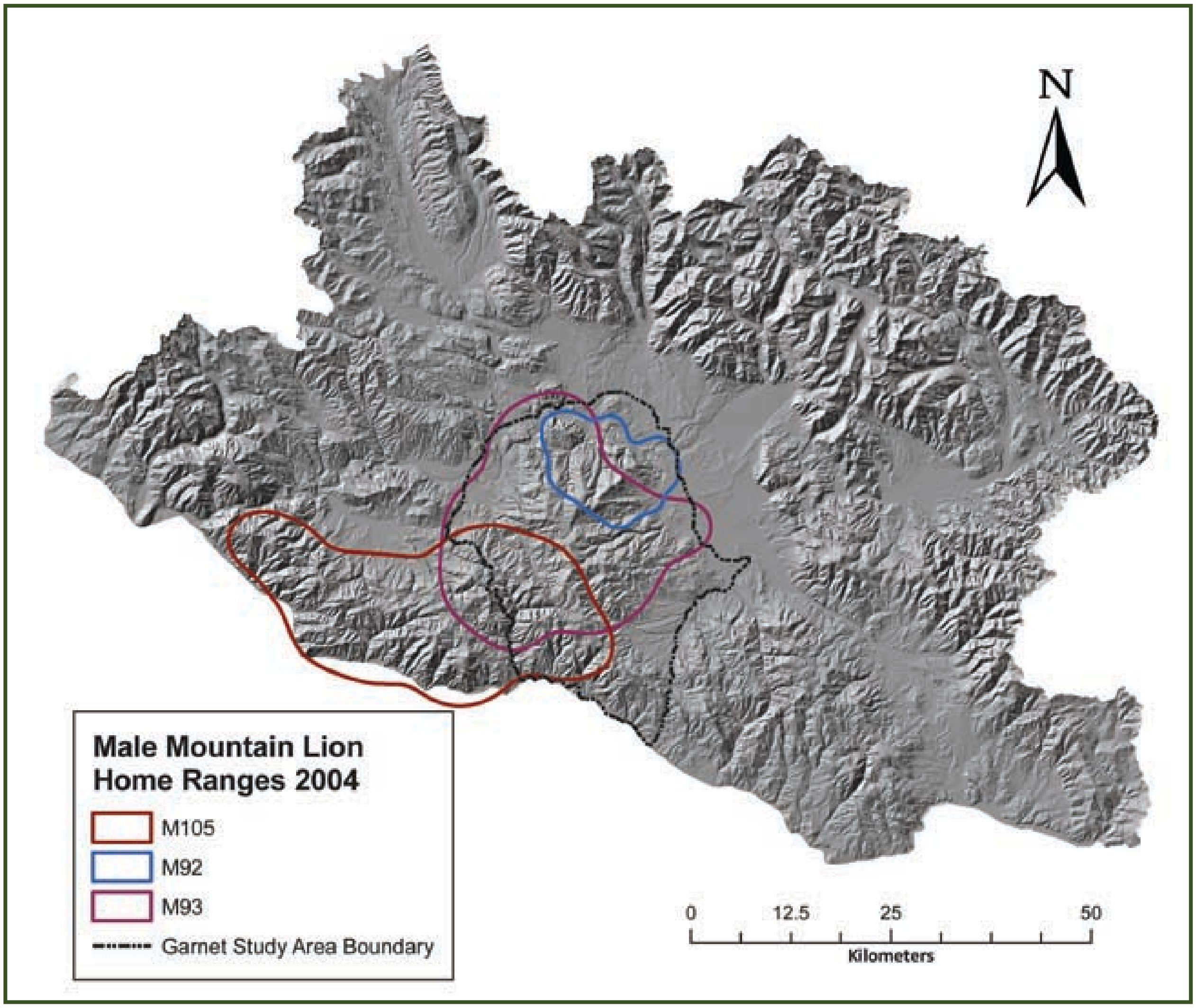


Figure 3.5 Male annual 95% fixed kernel home ranges during 2004. The year 2004 is displayed as an example of home range size and overlap as it was in this year when the greatest number of independent animals were monitored inside the Garnet study area, Montana.

larger for female lions in the hunted versus a non-hunted areas, although the effect was not statistically significant (F = 2.2, df = 1, P = 0.14). We found no effect of hunting on female home range overlap (F = 0.52, df = 1, P = 0.47) (Table 3.1). Male home ranges were larger on average when hunted, as predicted, however results were marginally significant between home range during the hunted and non-hunted periods (F = 14.78, df = 1, P = 0.06). Data were not sufficient to test for

	Hunted			Non hunted		
Home Range Size						
Sex	*n*	$\bar{x}$ (km^2)	95% CI	*n*	$\bar{x}$ (km^2)	95% CI
♀	13	386	275 - 496	50	246	188 - 303
♂	3	854	161 - 1547	6	603	193 - 1014
Overlap						
Sex	*n*	$\bar{x}$	95% CI	*n*	$\bar{x}$	95% CI
♀	13	0.34	0.27 – 0.41	50	0.32	0.27 – 0.38
♂	2	0.25	0.0 – 0.57	5	0.14	0.0 – 0.65

Table 3.1 Mean annual home range size and overlap in the Garnet study area pre and post protection from hunting.

differences in overlap of males, as only a single occurrence of two males with overlapping home ranges was found during the hunted period. Although the mean values of overlap were reduced in the non-hunted period, the 95% confidence intervals would suggest no difference between periods (Table 3.1).

We found no effect of hunting on maternity rates.

DISCUSSION

Our study population appeared to display the documented effects of hunting pressure that have also been shown elsewhere. While hunting directly reduced the density of the population from 37 to 20 animals between 1997 and 2000 (see also chapter 5), population parameters such as litter size, birth interval, maternity, age at dispersal and first breeding, as well as home range size and overlap where not significantly affected. Hunting pressure may have increased the proportion of adult males in the population, while reducing the average age of independent animals likely due to immigration into vacated home ranges; however neither affected the productivity of the population.

Uncollared female lion being treed by Spinner south of Missoula in the Missoula Special Management Area. (Photo courtesy of Bob Wiesner)

We estimated a mean litter size of between 2.35 and 2.93, dependent on how early the litter was first detected. Estimates of litter size have ranged from a low of 1.9 in Florida (Maehr and Caddick 1995) to a high of 3.1 in southeastern British Columbia (Spreadbury et al. 1996), with most averaging around 2.5 (Logan and Sweanor 2001). Murphy (1998), Logan and Sweanor (2001), and Cooley et al. (2009) have likely produced the least biased estimates of litter size by visiting den sites within the first 7 weeks of birth, producing means of 2.9 (n=15), 3.0 (n=53), and 2.55 (n=33) respectively. Both Murphy and Cooley et al. studied hunted populations. Similarly, our estimated birth interval of 19.8 months closely matched others in the literature, including 17.4 in (a non-hunted population) New Mexico (Logan and Sweanor 2001), 19.7 in Alberta (Ross and Jalkotzy 1992) and 24.3 in Utah (Lindzey et al. 1994).

We found no effect of hunting on maternity rates, and our mean maternity rate of 1.29 was similar to other published rates. Maternity in New Mexico (although referred to as fecundity) ranged from 1.3 to 1.6 kittens per female per year (Logan and Sweanor 2001), while Robinson et al. (2008) and Cooley et al. (2009) reported maternity rates in hunted populations of 1.2 and 1.1 kittens per female per year. The mean age of sires in our population, 35 months (range 15 – 57 months) was younger than others have reported elsewhere. For instance Logan and Sweanor (2001) found that 71% of litters in their non-hunted population were sired by males 35 to 88 months of age. However, our observed maternity rate and birth intervals suggest that the younger age structure of the male population during the hunted period did not affect kitten production.

Our mean age at dispersal of 15 months (range 11 to 23 months) was similar to other lion studies where dispersal occurred between 10 and 33 months (Sweanor et al. 2000). Levels of philopatry were also similar to non-hunted populations. Sweanor et al (2000), found that 68% of female recruits came from the local population, compared to our 50% philopatry rate in juvenile females. We documented 100% male juvenile dispersal following cessation of hunting pressure. Knopff (2010) had only one male mountain lion disperse out of his hunted study area, although his study area was twice the size of the Garnet.


Female mountain lion treed in the Missoula Special Management Unit south of Missoula. (Photo courtesy of Bob Wiesner)

Combining all animals during both the hunted and non-hunted periods we found mean annual home ranges of 275 km^2 and 687 km^2 for independent females and males respectively. Although differences in method used (i.e. kernel type and size, smoothing factor, etc.) make comparisons difficult, 12 lion studies in 9 states (using VHF collars and 90% fixed kernels) averaged 143 km^2 for female lion home ranges and 307 km^2 for male home ranges (Logan and Sweanor 2001, Ross and Jalkotzy 1992, Cunningham et al. 1995, Spreadbury et al. 1996, Hopkins 1989, Anderson et al. 1992, Seidensticker et al. 1973 Murphy 1983, Logan 1983). Perhaps more comparable are GPS based studies in hunted populations that found female 99% fixed kernel female home ranges of 249 km^2 and 199 km^2 and male home ranges of 753km^2 and 348 km^2 in heavily and lightly hunted populations, respectively (Maletzke 2010).

Female mountain lion home ranges are thought to be based on prey availability, while male home ranges are based on female availability, with breeding opportunities set by the number of females a male's home range overlaps (Ross and Jalkotzy 1992, Murphy 1998). In our study, relative prey availability should have been greatest during the hunting period as the mountain lion population was reduced, if prey numbers were relatively constant. However we found an opposite, although nonsignificant, trend with both male and female home ranges declining in size following the cessation of hunting. This finding would support the hypothesis


Biologist/houndsmen Grover Hedrick preparing to shoot immobilizing drug into adult female F84. (Photo courtesy of Melanie Trapkus)

that male home ranges are constricted at higher densities due to competition between males, supporting the male component of the two-strategies hypothesis, however our sample size and marginal statistical finding (*p*=0.06) does not allow us to support or refute this hypothesis.

Our most striking finding was the constraint on emigration during the heavy harvest period.

Perhaps our most striking finding of the effects of hunting on the characteristics of this hunted mountain lion population was the constraint on emigration during the heavy harvest period. Metapopulation dynamics are an increasingly important focus of mountain lion management and immigration and emigration have been shown to play a major role in balancing hunted and non-hunted mountain lion populations (Beier 1993, Robinson et al. 2008, Cooley et al. 2009). Harvest levels equivalent to those recorded during the first 3 years of our study may severely reduce a population's ability to act as a source of immigration to other areas, affecting not only the focal population level, but also those populations surrounding it.

Photo of front toes and pad of adult male M92. (Photo courtesy of Melanie Trapkus)

Biologists Vickie Edwards and Melanie Trapkus radio-collaring female kitten F96 at 7 months of age. (Photo courtesy of Grover Hedrick)

Biologist Melanie Trapkus drawing blood from radio-collared adult female F88. (Photo courtesy of Doug Powell)

Tooth wear and staining of adult male M92 (Photo courtesy of Melanie Trapkus)

SURVIVAL AND MORTALITY - SECTION 4

INTRODUCTION

Most mountain lion mortality is human related, whether accidental or deliberate. In populations that are protected from hunting, vehicle collisions and accidental poisoning are often the leading cause of mortality (Beier 1995, Taylor et al. 2002, Riley et al. 2007). In hunted mountain lion populations, the main source of mortality is invariably hunting (Ross and Jalkotzy 1992, Lambert et al. 2006, Knopff et al. 2010). Many wildlife agencies now employ a quota system where harvest is limited by season closure once a certain number of animals are taken. Female subquotas are generally set much lower than male or total quotas to reduce the impact of harvest on the population.

Radio-collared adult female F48. (Photo courtesy of Melanie Trapkus)

The effect of harvest on a population is dependent on total harvest rate, which age and sex classes are being harvested, as well as how harvest is compensated for by increases in survival or other vital rates (Mills 2007). Under the compensatory mortality hypothesis, harvest mortalities are compensated by density dependent decreases in nonharvest mortality allowing survival to remain constant (Williams et al. 2002). Evidence of the additive nature of hunting to mountain lion survival and population growth has been shown in past studies where populations were reduced through hunting, and/or increased once hunting pressure was reduced (Lindzey et al. 1992, Ross and Jalkotzy 1992, Lambert et al. 2006). Yet the question of whether or not hunting

The effect of harvest on a population is dependent on total harvest rate as well as how harvest is compensated for by increases in survival or other vital rates.

is compensatory continues to be raised (e.g.Quigley and Hornocker 2010), and the extent to which mountain lion populations are affected by hunting remains unclear.

Kitten survival is an often overlooked component of mountain lion harvest but may be affected in at least two ways.

Kitten survival is an often overlooked component of mountain lion harvest but may be affected in at least two ways. Logan et al. (1986) and Logan and Sweanor (2001) suggested that removal of male mountain lions from a population may decrease survival of resident males by disrupting social organization and increasing direct or exploitative competition for mates and territory. Cougars are considered to be infanticidal, where males may increase their breeding opportunities by inducing females into estrous by killing their kittens (Packer et al. 2009). A high level of turnover in males has been shown to result in increased levels of infanticide in African felids (Whitman et al. 2004, Balme et al. 2010). Although documented in cougar populations, it is yet unclear the role infanticide plays in shaping kitten survival.

Unlike ungulate species that give birth in a single "birth pulse" in early spring, thus ensuring independence of progeny during fall harvest, mountain lions give birth year round (see Section 3, figure 3.3) and are most heavily hunted from December to March. In non-hunted populations, kitten mortality is naturally high, especially during the first 6 months of life (Logan and Sweanor 2001). Harvest of female mountain lions during winter exposes dependent kittens to the risk of starvation due to abandonment, however, like adult mortality due to hunting, how this source of mortality is compensated for by decreases in other natural mortality is not well understood. Mortality of kittens may increase in hunted populations, not only directly from abandonment and starvation but from immigration of new infanticidal males.

Radio-collared adult female F84 was killed and eaten by newly arrived male M105. (Photo courtesy of Melanie Trapkus)

Five and one half month male kitten of F84 was killed and later eaten by male M105. (Photo courtesy of Melanie Trapkus)

Beginning in December 2000 the Garnet study area was managed separately from the remainder of the Blackfoot watershed. While the study area was mostly protected from hunting, with only single permits issued from 2003 to 2006, quotas in the remainder of the drainage were also reduced until female quotas were set to 0 in 2005 (Table 4.1). Protection of the Garnet study area was designed to allow for comparison to the previous hunted period, while the gradual reduction of quotas in the

Table 4.1. Mountain lion harvest quotas for Blackfoot river watershed Montana, 1998 to 2006. Years are based on a biological December to December year. Beginning in December 2000 the Garnet study area was managed separately from the remainder of the Blackfoot watershed.

	Sex	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Garnet managed as part of Blackfoot watershed.			0	0	0	1*	0	0
	Male				0	0	0	1*	1	1
Entire Blackfoot Drainage	Female	30	41	30	15	9	3	3	0	0
	Male	40	33	29	21	9	7	7	7	7

**1 either sex permit was issued for the Garnet in 2004*

remainder of the Blackfoot watershed was in response to growing concern by local houndsmen that the mountain lion population in that area was continuing to decline and quotas should be set that matched the decreasing number of animals.

Only 1 study animal was harvested inside the Missoula special management unit, therefore we used the harvest structure of the remainder of Blackfoot watershed to explore the effects of harvest and the efficacy of quota reductions in shaping mountain lion survival within that area. During the first 3 years of study the population in the study area in was reduced in order to gauge the level at which mortality became additive and population reduction could be achieved. Later protection of the Garnet study area allowed us to test the compensatory mortality hypothesis by comparing survival and cause specific mortality in spatially and temporally contiguous hunted and non-hunted areas. If we assume that natural and other non-hunting mortality sources operate in the same manner across the Blackfoot watershed, the compensatory mortality hypothesis suggests survival in the hunted and non-hunted portions of the drainage should be equal. In other words, survival should remain constant in non-hunted populations as other sources of mortality replace that attributable to harvest.

Our objective was to quantify and compare survival and cause specific mortality rates across the study period to determine if harvest structure, as regulated by MFWP, significantly impacted mountain lion survival. This analysis was also a necessary first step to determining the impact of hunting on population growth and dynamics (Chapter 5), in that results from this analysis provided guidance on how best to construct and parameterize population models.

Our objective was to quantify and compare survival and cause specific mortality rates across the study period.

Biologists Grover Hedrick, Rich DeSimone and Vickie Edwards viewing the remains of F84. (Photo courtesy of Melanie Trapkus)

METHODS

Survival Modeling

We modeled mountain lion survival using a combination of stepwise and best subsets model selection (Hosmer et al. 2008). First we conducted a univariate analysis using Cox regression (Cox 1972) to test the significance of sex, age, and hunting quota on mountain lion survival. Sex was coded as an indicator variable with females coded as 1 and males coded as 0. Age was coded as a continuous variable based on the estimated age of the animal in months. Quota was also coded as continuous based on the annual, sex, and location specific quotas as set by MFWP (see table 4.1).

We modeled mountain lion survival using a combination of stepwise and best subsets model selection.

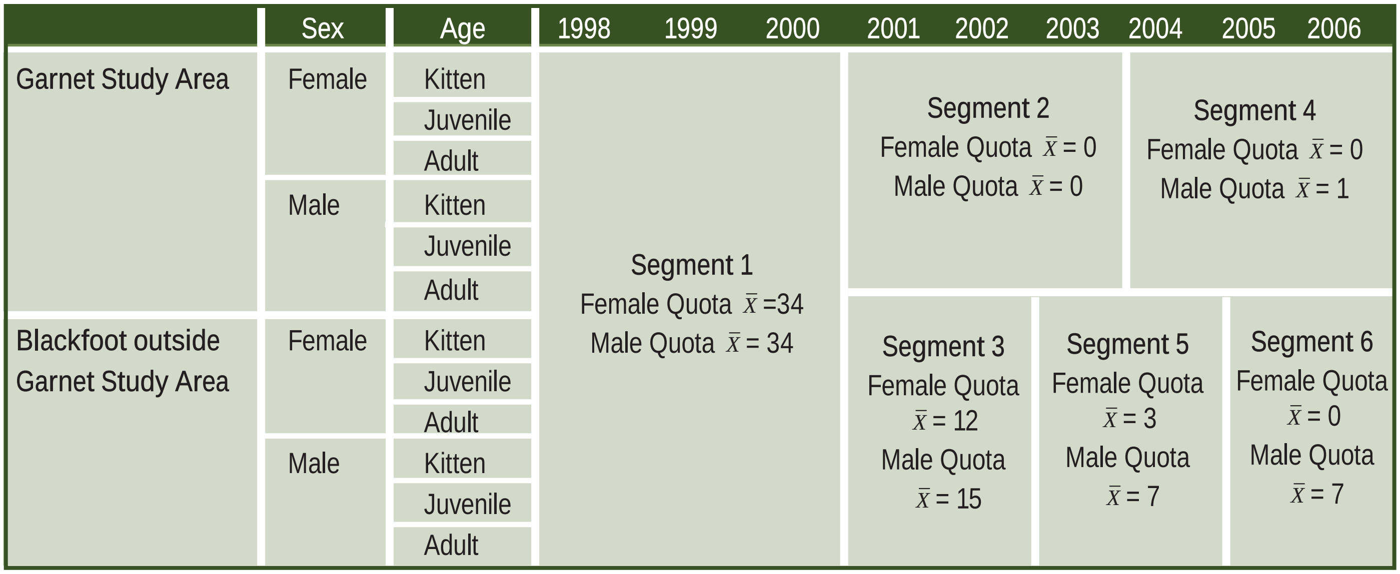
Secondly we modeled mountain lion survival on the landscape by constructing 11 spatial candidate models, each suggesting a different plausible survival pattern as a hypothesis (Figure 4.1 to Figure 4.12 – see figure caption for justification of each model's structure). For instance, the model "Pop_3" groups animals across the drainage between 1998 and 2000 (segment 1), then divides the population into two segments (segments 2 and 3) based on the protection of the Garnet study area following 2000, while hunting continued in the remainder of the Blackfoot drainage (Figure 4.5). This model tests the hypothesis that survival was equal across the Blackfoot prior to 2001, but differed significantly following closure of the Garnet despite gradual reductions in quota levels in the remainder of the watershed (Table 4.1). The "PopMan" model (Figure 4.1) tests the hypothesis that survival will respond to small incremental changes in management or quota level, thus dividing the population into 6 segments. We used Akaike's (AIC) and Bayesian information criterion (BIC) to select among competing models in order to evaluate the strength of evidence for each hypothesis regarding the relationship of survival to temporal and geographical quota levels, as well as age and sex (Burnham and Anderson 1998, Hosmer et al. 2008).

Radio-collared male M105 killed and ate adult female F84 and her kittens M104 and F100.
(Photo courtesy of Melanie Trapkus)

Although the Cox model makes no assumptions regarding the shape of the underlying hazard function in a survival model, it does require that each variable, or level of variable, have proportional hazard functions (Cleves et al. 2004). The spatial component in our survival models may induce a violation of the proportional hazards assumption, and negate the use of a traditional Cox model. We tested the proportional hazards assumption by graphing the hazard functions for mountain lions inside and outside the Garnet study area and examining the slope in a linear regression of the Schoenfeld residuals (Grambsch and Therneau 1994). Failing the proportional hazards assumption, we modeled survival time using a parametric Weibull distribution (Hosmer et al. 2008):

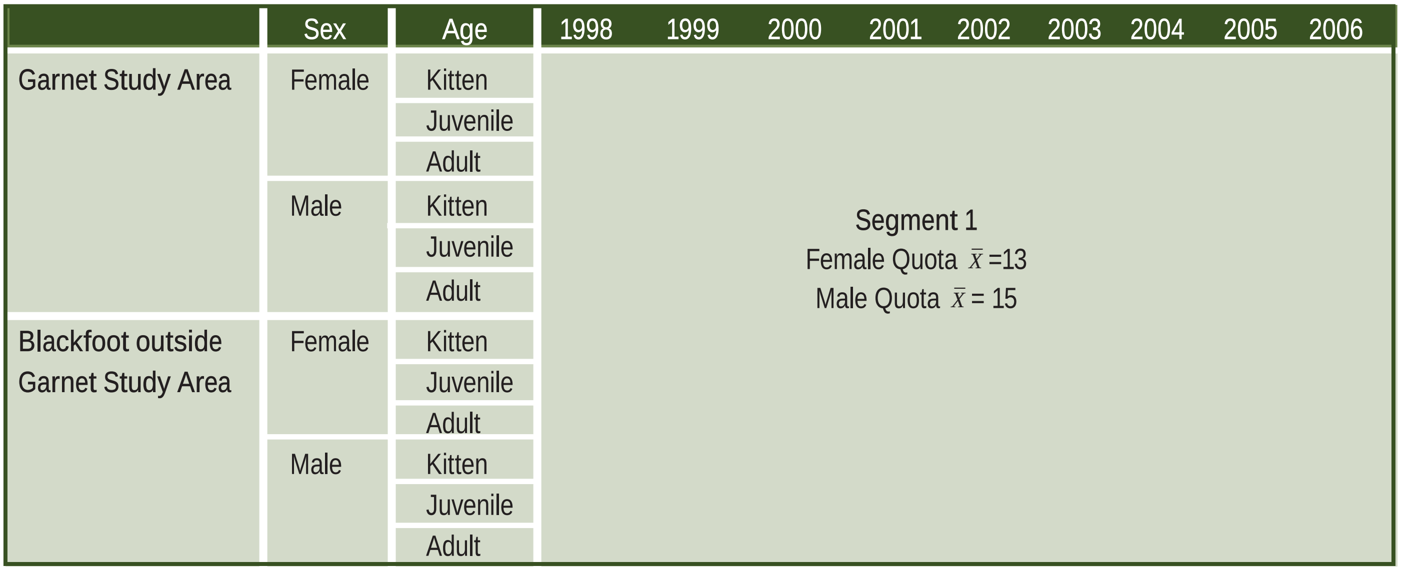
$$1n(T) = \beta_0 + \beta_1\chi + \sigma \times \varepsilon \qquad \text{(equation 4.1)}$$

where T is survival time, β_0 the model intercept, β_1 the covariate, σ a parameter estimating the shape of the hazard function based on the data, and ε the error term. Model parameterization was checked using a link test (Cleves et al. 2004).



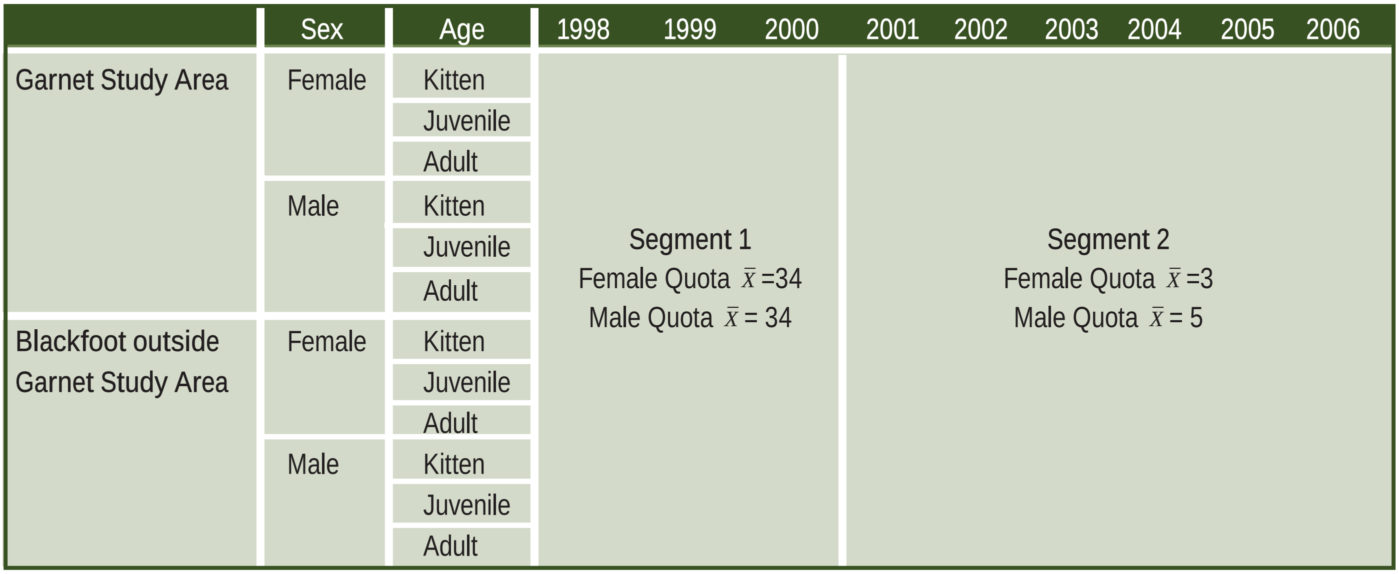
<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="12">Segment 1
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="3" rowspan="6">Segment 2
Female Quota $\bar{x}$ = 0
Male Quota $\bar{x}$ = 0</td><td colspan="3" rowspan="6">Segment 4
Female Quota $\bar{x}$ = 0
Male Quota $\bar{x}$ = 1</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="2" rowspan="6">Segment 3
Female Quota
$\bar{x}$ = 12
Male Quota
$\bar{x}$ = 15</td><td colspan="2" rowspan="6">Segment 5
Female Quota
$\bar{x}$ = 3
Male Quota
$\bar{x}$ = 7</td><td colspan="2" rowspan="6">Segment 6
Female Quota
$\bar{x}$ = 0
Male Quota
$\bar{x}$ = 7</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.1 . Management model (PopMan). Mortality in the Blackfoot watershed is modeled based on quotas set by Montana Fish Wildlife and Parks (see Table 4.1). This model tests the hypothesis that mountain lion population-level survival rates will respond to small incremental changes in quota levels.



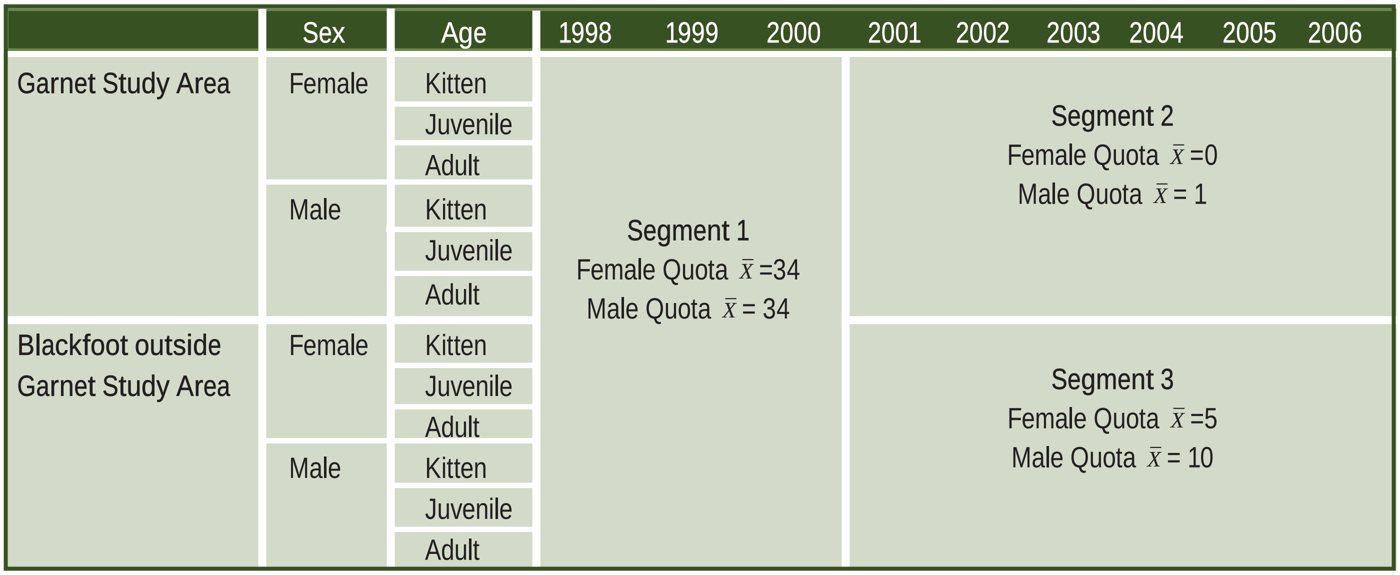
<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="9" rowspan="12">Segment 1
Female Quota $\bar{x}$ =13
Male Quota $\bar{x}$ = 15</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.2. Single population (pop_1) model. Mortality in the Blackfoot drainage is modeled as one open population with no spatial structure. This model hypothesizes no difference in survival between the Garnet Study Area and the remainder of the Blackfoot drainage across the study period, essentially that quota level and hunting does not affect mountain lion survival.



	Sex	Age	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Kitten	Segment 1 Female Quota $\bar{x}$ =34 Male Quota $\bar{x}$ = 34			Segment 2 Female Quota $\bar{x}$ =3 Male Quota $\bar{x}$ = 5					
		Juvenile									
		Adult									
	Male	Kitten									
		Juvenile									
		Adult									
Blackfoot outside Garnet Study Area	Female	Kitten									
		Juvenile									
		Adult									
	Male	Kitten									
		Juvenile									
		Adult									

Figure 4.3. Two population (pop_2) model. This model hypothesizes a difference in survival across the watershed following protection of the Garnet in December 2000, but that protection of the Garnet study area did not affect survival.



	Sex	Age	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Kitten	Segment 1 Female Quota $\bar{x}$ =34 Male Quota $\bar{x}$ = 34			Segment 2 Female Quota $\bar{x}$ =0 Male Quota $\bar{x}$ = 1					
		Juvenile									
		Adult									
	Male	Kitten									
		Juvenile									
		Adult									
Blackfoot outside Garnet Study Area	Female	Kitten				Segment 3 Female Quota $\bar{x}$ =5 Male Quota $\bar{x}$ = 10					
		Juvenile									
		Adult									
	Male	Kitten									
		Juvenile									
		Adult									

Figure 4.4. Three population (pop_3) model. This model assumes that survival was similar across the watershed prior to protection of the Garnet, but differed after December 2000.

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="6">Segment 1
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="6" rowspan="6">Segment 3
Female Quota $\bar{x}$ =0
Male Quota $\bar{x}$ = 1</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="7" rowspan="6">Segment 2
Female Quota $\bar{x}$ =19
Male Quota $\bar{x}$ = 21</td><td colspan="2" rowspan="6">Segment 4
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 7</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.5. Four population (pop_4) model. This model hypothesizes that survival was always significantly different in the Garnet study area compared to the rest of the Blackfoot watershed and following the cessation of hunting, and that survival was significantly different in remainder of the drainage only during the last two years of study when female quotas were reduced to 0.

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="12">Segment 1
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="4" rowspan="6">Segment 2
Female Quota $\bar{x}$ =0
Male Quota $\bar{x}$ = 1</td><td colspan="2" rowspan="12">Segment 4
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 7</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="4" rowspan="6">Segment 3
Female Quota $\bar{x}$ =8
Male Quota $\bar{x}$ = 11</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.6. Five population (pop_5) model. Similar to the pop_3 model with the added hypothesis that survival would be equivalent across the drainage once female quotas outside the Garnet study area were reduced to 0 matching those within.

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="6">Segment 1
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="3" rowspan="6">Segment 3
Female Quota $\bar{x}$ =0
Male Quota $\bar{x}$ = 0</td><td colspan="3" rowspan="6">Segment 5
Female Quota $\bar{x}$ =0
Male Quota $\bar{x}$ = 1</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="6">Segment 2
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="3" rowspan="6">Segment 4
Female Quota $\bar{x}$ =9
Male Quota $\bar{x}$ = 12</td><td colspan="3" rowspan="6">Segment 6
Female Quota $\bar{x}$ =1
Male Quota $\bar{x}$ = 7</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.7. Six population (pop_6) model. Testing a similar hypothesis to the pop_man model (Figure 4.2) but gives a different structure to the incremental reductions in hunting quota, including the issuance of a permit inside the protected Garnet during the last three years of study.

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="12">Segment 1
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="2" rowspan="6">Segment 2
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 0</td><td colspan="2" rowspan="6">Segment 4
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 1</td><td colspan="2" rowspan="6">Segment 6
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 1</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="2" rowspan="6">Segment 3
Female Quota
$\bar{x}$ =12
Male Quota
$\bar{x}$ = 15</td><td colspan="2" rowspan="6">Segment 5
Female Quota
$\bar{x}$ =3
Male Quota
$\bar{x}$ = 7</td><td colspan="2" rowspan="6">Segment 7
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 7</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.8. *Seven population (pop_7) model. Similar to the pop_man model however separates last 4 years of the study based on the either sex tag of 2004.*

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="12">Segment 1
Female Quota $\bar{x}$ =34
Male Quota $\bar{x}$ = 34</td><td colspan="2" rowspan="12">Segment 2
Female Quota
$\bar{x}$ =6
Male Quota
$\bar{x}$ = 8</td><td colspan="2" rowspan="12">Segment 3
Female Quota
$\bar{x}$ =2
Male Quota
$\bar{x}$ = 4</td><td colspan="2" rowspan="12">Segment 4
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 4</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.9. Eight population (pop_8) model. This model was developed to test if significant reductions in female quotas in the last 4 years of study where sufficient to equate survival in the protected Garnet and the remainder of the Blackfoot watershed

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td>Watershed</td><td>Combined</td><td>Kitten</td><td colspan="9">Segment 1</td></tr>
<tr><td rowspan="5">Garnet Study Area</td><td rowspan="2">Female</td><td>Juvenile</td><td colspan="3" rowspan="11">Segment 2</td><td colspan="4" rowspan="5">Segment 3</td><td colspan="2" rowspan="11">Segment 5</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="4" rowspan="6">Segment 4</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.10. Kitten population model (popkit). Tested the hypothesis that kitten survival did not vary across years. Selection of this as the top model would suggest that kitten survival was constant while juvenile and adult survival varied based on quotas.

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td>Watershed</td><td>All Kittens</td><td></td><td colspan="9">Segment 1</td></tr>
<tr><td rowspan="2"></td><td rowspan="2">Male</td><td>Juvenile</td><td colspan="9" rowspan="2">Segment 2</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="2">Garnet Study Area</td><td rowspan="2">Female</td><td>Juvenile</td><td colspan="3" rowspan="4">Segment 3</td><td colspan="4" rowspan="2">Segment 4</td><td colspan="2" rowspan="4">Segment 6</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="2">Blackfoot outside Garnet Study Area</td><td rowspan="2"></td><td>Juvenile</td><td colspan="4" rowspan="2">Segment 5</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.11. Male population (popmale) model. Tested the hypothesis that the garnet study area provided a refuge for females, however was too small to increase male survival.

<table>
<tr><th></th><th>Sex</th><th>Age</th><th>1998</th><th>1999</th><th>2000</th><th>2001</th><th>2002</th><th>2003</th><th>2004</th><th>2005</th><th>2006</th></tr>
<tr><td rowspan="6">Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="3" rowspan="12">Segment 1
Female Quota $\bar{x}$ =23
Male Quota $\bar{x}$ = 25</td><td colspan="4" rowspan="6">Segment 2
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 1</td><td colspan="2" rowspan="12">Segment 3
Female Quota
$\bar{x}$ =0
Male Quota
$\bar{x}$ = 4</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="6">Blackfoot outside Garnet Study Area</td><td rowspan="3">Female</td><td>Kitten</td><td colspan="4" rowspan="6"></td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
<tr><td rowspan="3">Male</td><td>Kitten</td></tr>
<tr><td>Juvenile</td></tr>
<tr><td>Adult</td></tr>
</table>

Figure 4.12. Hunting population (pophunt) model, similar to the pop_man model (Figure 4.1) this model suggests that survival was similar in the Blackfoot and Garnet prior to protection and equal again once quotas were restricted in the Blackfoot following 2004.

Survival Analysis

Here we used survival analysis to calculate the survival rates or probabilities of those same groups from the top models.

Survival modeling in the previous section was similar to any regression modeling of the relationship between an outcome variable, in this case death, and one or more independent variables or covariates. In this section we conducted a survival analysis, as opposed to survival modeling, which is the quantification of the probability of an individual's survival based on their cohort (i.e. age or sex classification). Although related, the two analyses are separate. We used survival modeling in the previous section to determine the best method of breaking the population into segments or cohorts with similar survival experiences. Here we used survival analysis to calculate the survival rates or probabilities of those same groups from the top models.

Early in the study, VHF collars were employed to monitor mountain lions, and marked animals were located on approximately a weekly basis. Beginning in 2001, GPS collars programmed to acquire a location every 5 hours were employed to monitor mountain lions, and crews replaced VHF collars on already marked animals as opportunity allowed. We derived an encounter record for survival analysis from these telemetry data. Duplicate, same day, locations where removed from GPS collar data and combined with VHF data to create a continuous record based on days for each animal.

The use of telemetry data in survival analysis requires combining single observations into a measure of time at risk, and mortality events. In non-parametric analysis, pairs of records (i.e. an observation at time t and a second observation at time t+1) and their associated variables, form the basis of the analysis. Variables associated with each animal then must be defined as enduring (valid across a specific time span), or event (events that occurred at that instant). For this analysis, because encounters were recorded in days, age (measured in months) was considered enduring, while location was considered an event variable (Johnson et al. 2004). This has the effect that age was considered constant across individual spans (value obtained from the start of the span), while location was measured from the second observation (the animal was assumed to have spent the span in the location it was found – i.e. either in or out of the Garnet study area). Animals that were not located for longer than 61 days were interval truncated/censored (temporarily removed from analysis) until relocated (Winterstein et al. 2001).

The Kaplan-Meier product limit estimator (Kaplan and Meier 1958) has gained wide acceptance in wildlife studies exploring survival of radio-collared animals. The Kaplan-Meier estimator produces a survival rate for distinct intervals based on the difference between the number of animals at risk and the number of mortalities, divided by the total number of animals at risk for that interval. The survival rate for a given span is then the product of each interval. For this reason, the estimator is sensitive to small sample sizes, a single interval where no other animals are at risk produces a zero which is then carried through the rest of the span regardless of more animals being added per usual in a staggered entry design. The Nelson-Aalen estimator is analogous to the Kaplan-Meier but is less sensitive to small sample sizes (Murray 2006). The Nelson-Aalen estimator produces a hazard function which can then be converted back to a

The use of telemetry data in survival analysis requires combining single observations into a measure of time at risk, and mortality events.

Biologists Vickie Edwards listening for the signal of radio-collared female F96 and Grover Hedrick recording tracks on the Potter Mountain Lion Track Route. (Photo courtesy of Melanie Trapkus) survival rate equivalent to a Kaplan-Meier survival rate using:

$$S_t = \exp\left(-H_t\right)$$

(equation 4.2)

where S_t is the probability of survival to time (*t*) and H_t is the Nelson-Aalen hazard at time (*t*).

We calculated cause-specific mortality rates using cumulative incidence functions (CIFs).

We calculated annual survival rates for 3 age classes of mountain lions; kitten (1-12 months), juvenile (13-24 months), and adult (>25 months) for each population model segment (as delineated by our a priori model selection, see above) using the Nelson-Aalen estimator (Nelson 1972, Aalen 1978). Survival rates were based on a biological December to December year (i.e. the cumulative hazard estimate for each segment was raised to the power of 1/t, where t represents the length of that period in years, in order to calculate a mean annual survival rate across that period).

Several methods have been proposed to test for differences in survival including likelihood ratio tests, log-rank tests, or Wilcoxon tests (Hosmer et al. 2008). The power of these tests to detect significant differences in survival has been questioned, especially where animals or populations come under different patterns of censoring (Murray 2006). To test for significant differences in survival between the various segments of the population we used a Peto-Prentice test (Peto and Peto 1972, Prentice 1978) which is less susceptible to differences in censoring patterns (Hosmer et al. 2008).

Cause Specific Mortality

We calculated cause-specific mortality rates using cumulative incidence functions (CIFs) (Kalbfleisch and Prentice 1980, Heisey and Patterson 2006). CIFs allow the estimation of mortality rates in the presence of competing risks; more than one, mutually exclusive, cause of death (Pintilie 2006). Unlike the modified Mayfield or Heisey-Fuller (Mayfield 1961, Heisey and Fuller 1985) method of mortality estimation which assume a normal or constant distribution of mortality risk, CIFs make no assumption regarding the underlying hazard distribution. However, due to their prevalence in past studies, we also present cause-specific mortality rates calculated using the Heisey-Fuller method and program Micromort (Heisey and Fuller 1985).

We grouped mortalities by 6 causes. Animals that were harvested as part of a legal hunt, or kittens

Radio-collared male kitten M99 at 7 1/2 months of age. (Photo courtesy of Melanie Trapkus) that were orphaned and starved after their mothers were shot where classified as hunting mortality. Illegal mortality included animals killed in snares or otherwise killed out of season. Animals that died naturally due to starvation, disease, or intraspecific strife (including cases of infanticide) were classified as natural mortalities. The category depredation included animals shot due to conflict with humans (i.e. livestock depredation permits, and self defense). The final two categories were vehicle collisions and unknown, where a clear cause of death could not be determined.

We tested the compensatory hunting mortality hypothesis in two ways. First we regressed survival of independent mountain lions against hunting mortality; kittens were omitted due to their non-independence from adult females. If hunting was compensatory we would expect survival to remain constant as hunting mortality increased. Conversely if hunting mortality was additive, we would expect a monotonic decrease in survival with an increase in hunting mortality (Williams et al. 2002). This regression used survival and hunting mortality probabilities based on the Popman model population structure (i.e. 6 population segments based on varying hunting quota levels, see Figure 4.1). A similar analysis could have been conducted on annual survival and mortality values (e.g. Murray et al. 2010). However, as the management goal during the first three years of the study was to reduce the population, almost ensuring additive mortality, using annual rates may have biased our analysis towards an additive finding. Although using the Popman model reduces the number of data point to 6 from the 9 available in an annual analysis, we believe this structure less biased towards an additive finding as the first three years of mortality are captured in a single data point while at the same time providing a mixture of hunting and natural mortality based on the protected and hunted portions of the Blackfoot watershed following December 2000.

We tested the compensatory hunting mortality hypothesis in two ways.

Secondly we tested the compensatory mortality/infanticide hypothesis in adult and kitten survival by comparing the cumulative incidence functions (CIF) for hunting and all other mortality sources between the hunted and non-hunted periods. Pepe and Mori (1993) give a method for comparing the CIFs of a main mortality source and competing risks simultaneously between two groups (i.e. hunting mortality in a heavily hunted vs. lightly hunted population and remaining competing risks across those same populations). This tests the hypothesis of equality in the CIF of a main event or event of interest (i.e. hunting mortality) between two groups while also testing for equality in the remaining competing risks (Pintilie 2006). If hunting mortality

Immobilized five month old kittens of radio-collared female F35. (*Photo courtesy of Melanie Trapkus*) was additive, we would expect an increase in the hunting CIF while the CIF for competing risks remained constant or was lower in the non-hunted population. Conversely, if hunting mortality was compensatory, we would expect an increase in the hunting CIF, with a concurrent reduction in mortality due to competing risks in the hunted population.

Of 121 collared mountain lions, we documented 63 mortalities between January 1998 and December 2006.

RESULTS

Of 121 collared mountain lions, we documented 63 mortalities between January 1998 and December 2006. Two other known mortalities were excluded from our analysis as they occurred following cessation of field activities in January 2007. Mortalities were recorded in every month but October, with the majority coinciding with the start of the hound hunting season in December (Figure 4.13).

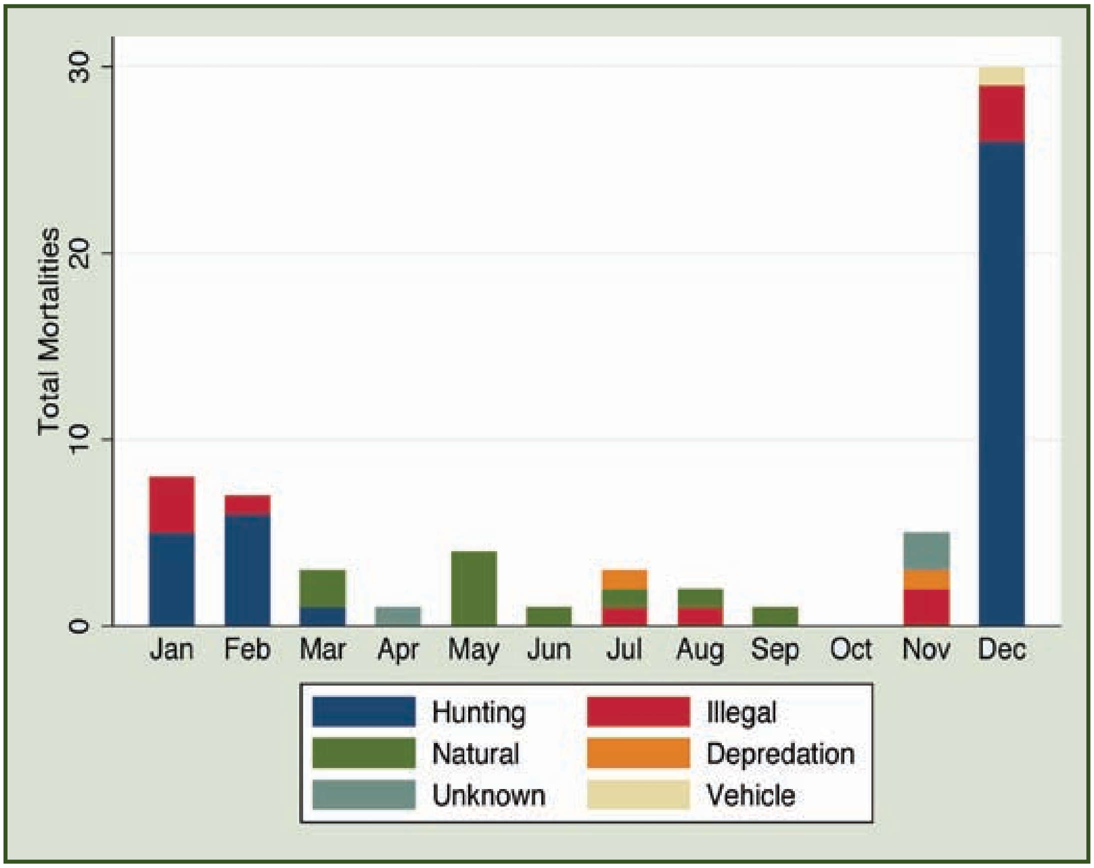


Figure 4.13 Timing and cause of 63 radio collared mountain lion mortalities 1998 to 2006, Blackfoot river watershed, Montana.

Survival Modeling

Sex was the best predictor of mountain lion survival followed by quota and age. Females where 73% less likely than males to die, a mountain lion's risk of mortality increased 10% with each unit increase in quotas, and risk of mortality was highest for kittens, declining by 1% for each month survived (Table 4.2 and Figure 4.14). While age was not a significant model covariate at the 0.05 level, Hosmer and Lemeshow (2000) recommend retaining variables with a probability of significance of 20% (P = 0.2) for inclusion in further modeling following univariate analysis. This, as well as our desire to create age based population models as the next phase of our research (Section 5) dictated the inclusion all three variables in our subset models, with age broken into 3 and 4 categories (see Section 4 - Survival Analysis).

Graphing the smoothed hazard functions for areas within and outside the Garnet study area suggested that the proportional hazard assumption did not hold (Figure 4.15). A test of the Schoenfeld residuals for mortalities inside and outside the Garnet showed only weak support of proportional hazard assumption ($\chi^2 = 1.70$, df = 1, $P = 0.19$). A graph of the same residuals displayed a distinct slope in trend (Figure 4.16). Tests of the subset models (i.e. Pop_3, Popman, etc.) performed even worse (e.g. Pop_3 global model, $\chi^2 =$

Table 4.2. Univariate analysis of sex, age, and quota level on survival of mountain lions in the Blackfoot watershed, western Montana 1998 to 2006.

Variable	Hazard Ratio	S.E.	z	P>|z|	AIC
Sex	0.2749	0.074	-4.79	<0.01	345.07
Quota	1.10	0.039	2.77	<0.01	359.17
Age	0.9929	0.004	-1.52	0.11	364.39

10.66, df = 4, *P* = 0.03). These combined results suggested that a parametric model, in this case the Weibull distribution, was better suited for this analysis.

Two models, Pop_3 and Pop_4, including 3 age classes and sex, were considered the top models (Table 4.3, Figure 4.4 and Figure 4.5). The same population structures with an added age classification for subadults were considered the 3rd and 4th best models. Differences in AIC values of less than 2 are normally considered too low to distinguish between models, although models with fewer parameters may be preferred (Burnham and Anderson 2002). Despite the pop_3age4 model being within a delta AIC value of 2 of the top model, the added degree of freedom for a fourth age classification made it less parsimonious and therefore less desirable. The popman model, which mimicked the actual quota levels, was the 7th ranked model (Table 4.3, Figure 4.2).

A linktest showed that both the Pop_3 (Z= -0.51 P = 0.61), and Pop_4 (Z = -0.58 P = 0.56) models were properly parameterized. Of note, the Pop_1 model included mainly for interest, was possibly under parameterized as shown by its weaker level of non-significance (Z = 1.24, P = 0.21).

Survival Analysis

Mean annual survival, pooling all individuals across all years, was 0.6511 (Table 4.4). Male and female survival of kittens and juveniles did not differ (kitten $\chi^2 = 0.14$, $df = 1$, $P = 0.70$; juvenile

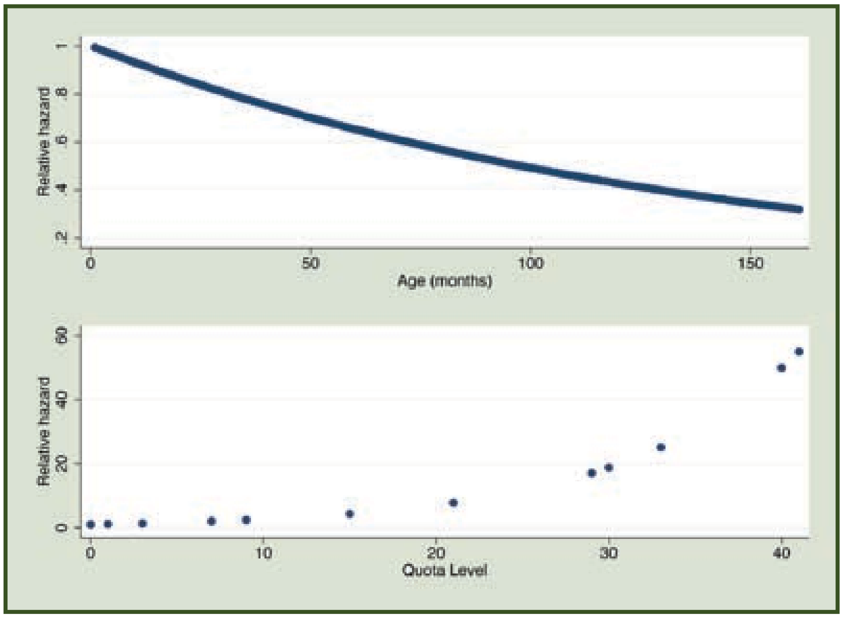


Figure 4.14 Changes in relative hazard with age and quota level for mountain lions, Blackfoot watershed western Montana 1998 to 2006.

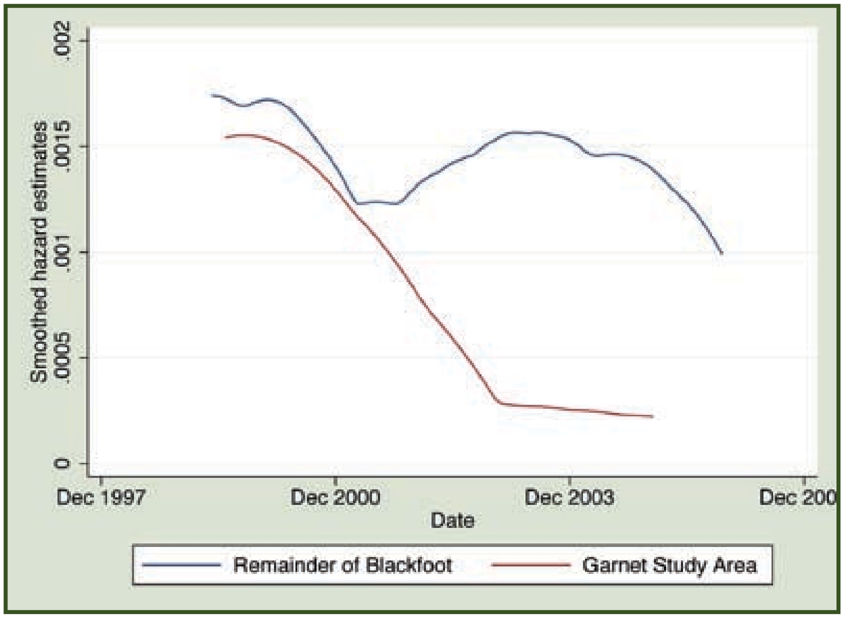


Figure 4.15 Smoothed hazard functions for areas within, and outside the Garnet study area. Divergence of the hazard functions denotes the reduced hazard with protection of the Garnet beginning in December 2000.

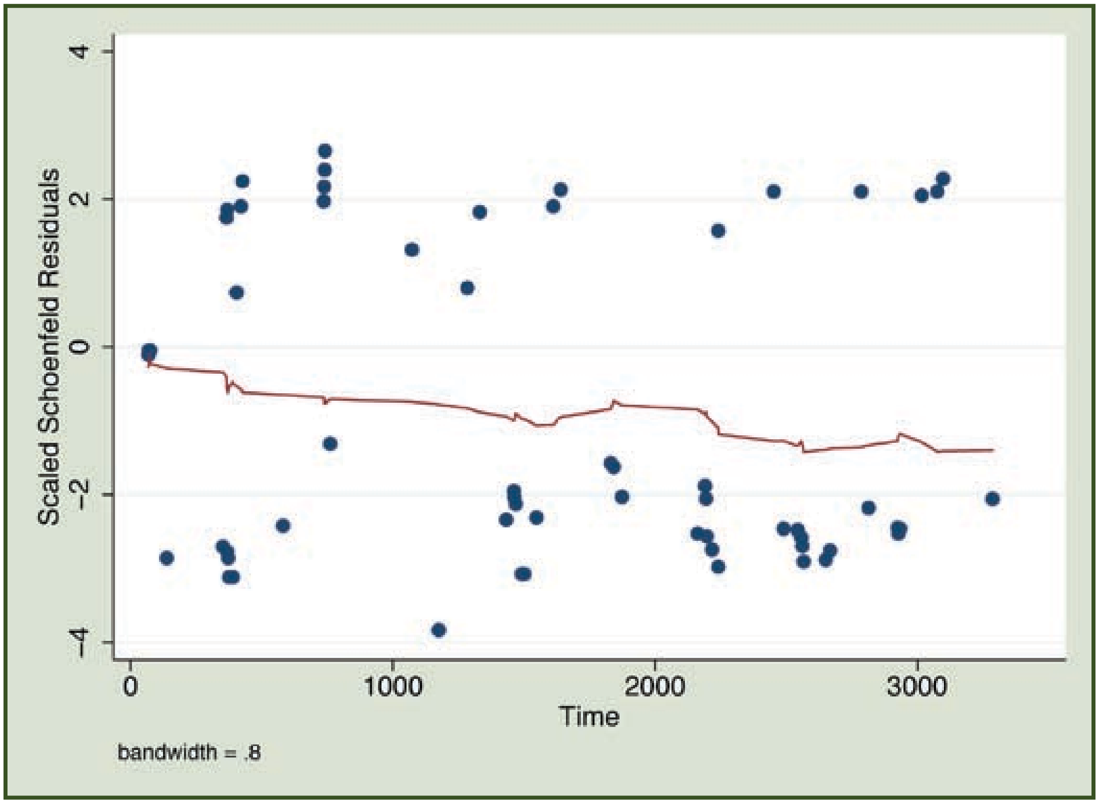


Figure 4.16. Schoenfeld residuals from mountain lion mortalities in Montana (1998-2006) fitted to a Cox proportional hazard model of locations inside and out of the Garnet study area. Parallel clustering of the residuals is a function of the two study areas, while the significant negative slope of the best fit line belays a non-proportional (i.e. unequal) hazard function between the two areas over time.

Only adult survival was significantly different between sexes.

$\chi^2 = 0.18$, $df = 1$, $P = 0.66$). Only adult survival was significantly different between sexes ($\chi^2 = 5.04$, $df = 1$, $P = 0.02$).

Adult survival was similar between the Garnet study area and the remainder of the Blackfoot drainage prior to December 2000 ($\chi^2 = 0.45$, $df = 1$, $P = 0.50$), but differed significantly once hunting was halted in the Garnet ($\chi^2 = 17.62$, $df = 1$, $P < 0.01$) (Table 4.5 and 4.6). Once adult female quotas were reduced to 0 outside the Garnet study area (population segment 4 of the pop_4 model, see Figure 4.6) adult survival increased marginally ($\chi^2 = 3.08$, $df = 1$, $P = 0.08$) compared to survival prior (population segment 2). The marginal significance in total adult survival is explained by an increase in adult female survival while adult male survival remained relatively constant (Table 4.7). These similarities and disparities in adult survival are reflected in the selection of the Pop_3, and Pop_4 models as best describing the survival structure in the Blackfoot watershed between 1998 and 2006 (Table 4.3).

Cause Specific Mortality

Hunting was the main cause of mortality for all age and sex classes across the study period, accounting for 36 of 63 mortalities documented. This was followed by illegal mortalities, natural, unknown, depredation, and vehicle collision mortalities (Table 4.8). Across the study period, any lion in the Blackfoot watershed had on average a 22% annual probability of dying due to hunting. Regression

Table 4.3. Models considered in best fit analysis of mountain lion mortality patterns in Blackfoot watershed Montana 1998 – 2006. Null model log likelihood was -54.2168 and all models were based on 17245 observations.

Rank	Model	LL Model	df	AIC	BIC	ΔAIC	ΔBIC
1	pop3age3	-35.8489	7	85.69773	139.9847	0	4.2601
2	pop4age3	-35.258	8	86.51594	148.5582	0.81821	12.8336
3	pop3age4	-35.6454	8	87.29086	149.3331	1.59313	13.6085
4	pop4age4	-35.1461	9	88.29215	158.0897	2.59442	22.3651
5	popHage3	-37.4259	7	88.85185	143.1388	3.15412	7.4142
6	pop5age3	-37.2123	8	90.42451	152.4667	4.72678	16.7421
7	popman3	-35.2133	10	90.4265	167.9793	4.72877	32.2547
8	popMale	-38.2691	7	90.53825	144.8252	4.84052	9.1006
9	popHage4	-37.3514	8	90.70271	152.7449	5.00498	17.0203
10	pop6age3	-35.6565	10	91.31302	168.8658	5.61529	33.1412
11	popKit	-38.6911	7	91.38225	145.6692	5.68452	9.9446
12	popman4	-35.0569	11	92.11375	177.4218	6.41602	41.6972
13	pop5age4	-37.0875	9	92.17496	161.9725	6.47723	26.2479
14	pop7age3	-35.1752	11	92.35046	177.6585	6.65273	41.9339
15	pop6age4	-35.4414	11	92.88276	178.1908	7.18503	42.4662
16	pop7age4	-35.0113	12	94.02267	187.086	8.32494	51.3614
17	pop1age3	-43.4741	5	96.9482	135.7246	11.25047	0
18	pop2age3	-43.3312	6	98.66238	145.194	12.96465	9.4694
19	pop1age4	-43.3771	6	98.75419	145.2859	13.05646	9.5613
20	pop2age4	-43.2626	7	100.5252	154.8121	14.82747	19.0875
21	pop8age3	-43.0002	8	102.0003	164.0425	16.30257	28.3179

Table 4.4 Mean annual survival rates of radio-collared mountain lions 1998 to 2006, western Montana. Only adult survival differed between sexes.

Sex	Age Class	Survival	SD	Lower 95% CI	Upper 95% CI
Female	Kitten	0.8776	0.05	0.7438	0.9439
	Juvenile	0.7274	0.11	0.4543	0.8795
	Adult	0.7865	0.05	0.6784	0.8619
Male	Kitten	0.75	0.08	0.5666	0.8668
	Juvenile	0.4886	0.26	0.2571	0.6854
	Adult	0.5150	0.12	0.2574	0.7229

Table 4.5 Mean survival rates (and standard deviations) of radio-collared mountain lions based on management (PopMan) model.

	Sex	Age	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Kitten	Survival pooled across Watershed.			0.9459 (0.10)			1.0		
		Juvenile				1.0			1.0		
		Adult				1.0			0.9321 (0.04)		
	Male	Kitten				0.5427 (0.18)			0.8234 (0.10)		
		Juvenile				1.0			1.0		
		Adult				1.0			0.6068 (0.17)		
Blackfoot outside Garnet Study Area	Female	Kitten	0.7765 (0.10)			1.0		1.0		0.7788 (0.19)	
		Juvenile	0.4859 (0.16)			0.8464 (0.16)		1.0		0.7788 (0.19)	
		Adult	0.6737 (0.09)			0.6872 (0.17)		0.5108 (0.14)		0.8746 (0.09)	
	Male	Kitten	0.7619 (0.11)			1.0		1.0		1.0	
		Juvenile	0.3892 (0.16)			0.3678 (0.19)		0.6596 (0.18)		0.3384 (0.16)	
		Adult	0.7167 (0.21)			0.3998 (0.18)		0.4728 (0.20)		0.5488 (0.21)	

Table 4.6. Mean annual survival rates of collared mountain lions broken into population segments according to our pop_3 model structure.

	Sex	Age	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Kitten	Survival pooled across Watershed.			0.9726 (0.04)					
		Juvenile				1.0					
		Adult				0.9654 (0.03)					
	Male	Kitten				0.6686 (0.13)					
		Juvenile				1.0					
		Adult				0.7789 (0.15)					
Blackfoot outside Garnet Study Area	Female	Kitten	0.7765 (0.10)			0.9201 (0.11)					
		Juvenile	0.4859 (0.16)			0.8704 (0.10)					
		Adult	0.6737 (0.09)			0.7131 (0.08)					
	Male	Kitten	0.7619 (0.11)			1.0					
		Juvenile	0.3892 (0.16)			0.4347 (0.13)					
		Adult	0.7167 (0.21)			0.4699 (0.14)					

analysis of hunting-caused mortality and survival of juveniles and adults showed a significant negative slope ($F = 21.97$, $df = 5$ $P = 0.01$), consistent with the additive hunting mortality hypothesis (Figure 4.17). For adults and juveniles, PepeMori tests of equality in mortality rates between hunted and non-hunted segments of the population were significant (hunting mortality χ^2=31.18, $P < 0.01$, all other mortality χ^2=3.58, $P = 0.06$). The significant difference in other mortality sources between hunted and non-hunted populations was due to higher mortality in the hunted populations, supporting the additive hunting mortality hypothesis (Figure 4.18).

Table 4.7 Mean annual survival rates of collared mountain lions divided by pop_4 population structure.

	Sex	Age	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	Female	Kitten	0.7765 (0.10)			0.9726 (0.04)					
		Juvenile	0.7576 (0.15)			1.0					
		Adult	0.5740 (0.14)			0.9654 (0.03)					
	Male	Kitten	1.0			0.6686 (0.13)					
		Juvenile	0.3892 (0.16)			1.0					
		Adult	1.0			0.7789 (0.15)					
Blackfoot outside Garnet Study Area	Female	Kitten	1.0							0.7788 (0.20)	
		Juvenile	0.7883 (0.13)							0.7788 (0.20)	
		Adult	0.59 (0.11)							0.8746 (0.10)	
	Male	Kitten	0.7167 (0.13)							1.0	
		Juvenile	0.6674 (0.14)							0.3384 (0.16)	
		Adult	0.5387 (0.13)							0.5488 (0.21)	

Table 4.8 Cause specific mortality rates of radio-collared mountain lions 1998 to 2006, Blackfoot river watershed, Montana (Heisey-Fuller mortality rates calculated using program Micromort are included for comparison although CIFs were used in all further analysis) .

				Cause			
Age Class	Sex	Hunting	Illegal	Natural	Depredation	Unknown	Vehicle
Kitten	Male	2		5	1		1
	Female	4		2			
Juvenile	Male	9	2		1		
	Female	4	1			1	
Adult	Male	8	2				
	Female	9	6	3		2	
Total		36	11	10	2	3	1
Micromort		0.1664	0.0508	0.0462	0.0092	0.0138	0.0046
(variance)		(6x10^{-4})	(2x10^{-4})	(2x10^{-4})	(6x10^{-5})	(6x10^{-5})	(2x10^{-5})
CIFs		0.2212	0.0553	0.0380	0.0077	0.0114	0.0066
(SE)		(0.03)	(0.01)	(0.01)	(0.006)	(0.006)	(0.006)

During the heavy hunting period, prior to closure of the Garnet study area, 6 kittens died of starvation following the harvest of their mothers, a cause specific mortality rate of 0.41 (SE = 0.14). During the same period no kittens died of natural mortality, however following closure of the Garnet study area 7 kittens died of natural causes including 5 from cannibalism or infanticide and 2 of starvation, a cause specific mortality rate of 0.16 (SE = 0.06) (Figure 4.19). Kitten mortality attributed to hunting was higher during the 3 year period of

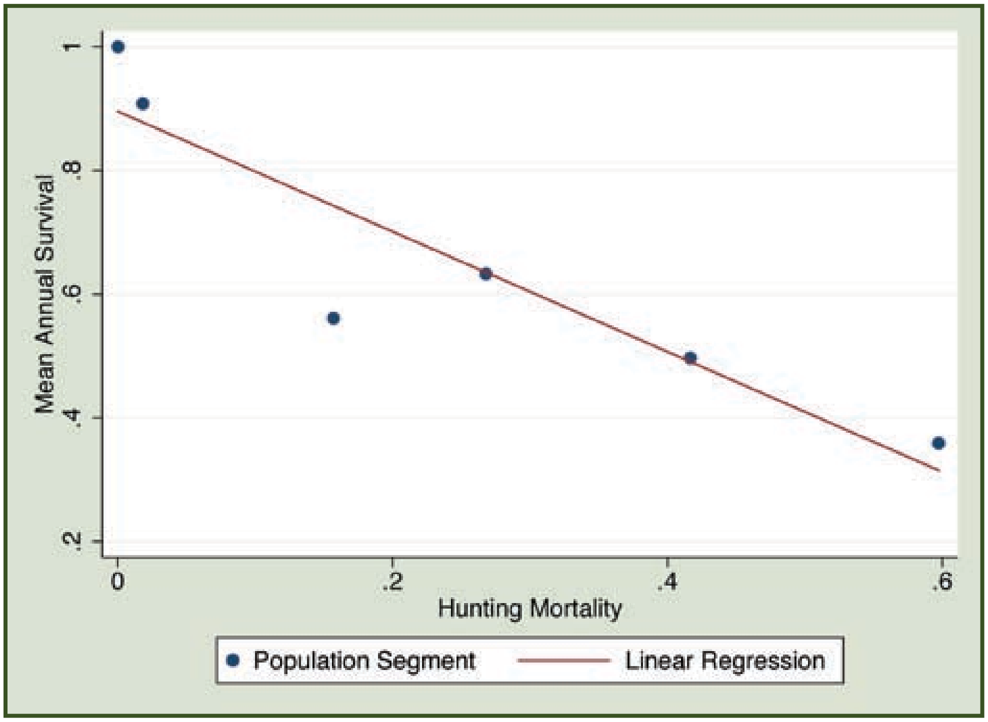


Figure 4.17. Hunting mortality and survival of adults and juveniles based on the management (popman) model population breakdown (see figure 4.1). A significant negative slope suggests hunting is an additive form of mortality (F = 21.97, df = 5 P = 0.01).

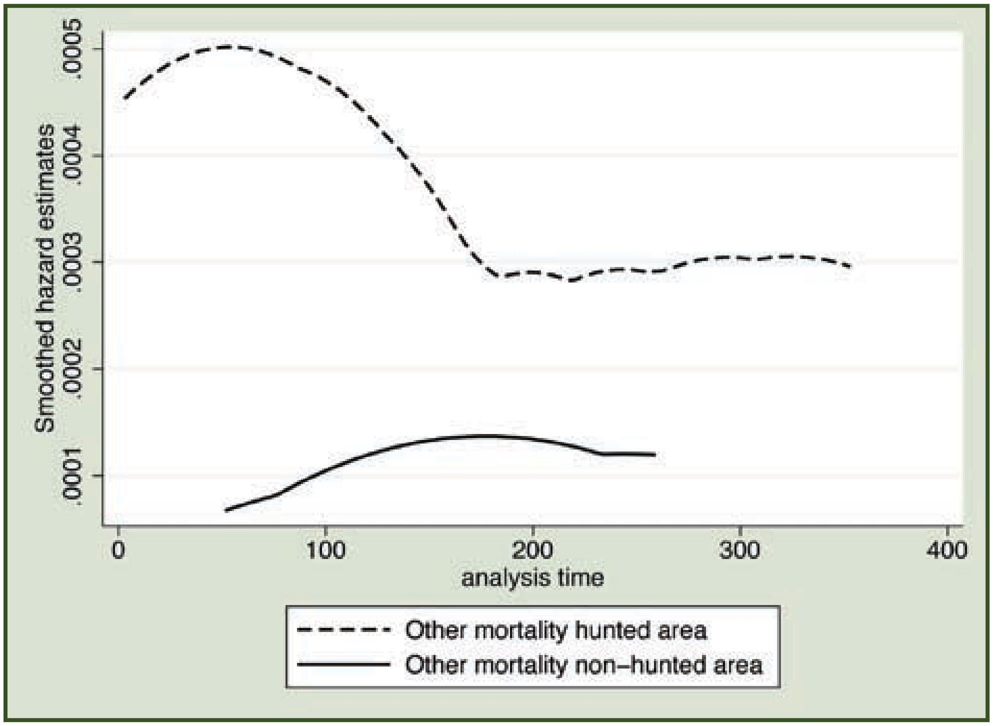


Figure 4.18. Hazard functions of all other mortality sources, excluding hunting, for adult and juvenile mountain lions in hunted and non-hunted population segments. A significantly lower probability of mortality from other sources in the absence of hunting ($\chi^2 = 3.58$, $P = 0.06$) does not support the compensatory hunting mortality hypothesis.

heavy hunting than in the 6 years following protection of the Garnet study area ($\chi^2 = 7.58$, $P = 0.01$). More importantly however, there was no change in all other sources of mortality between the two periods ($\chi^2 = 0.49$, $P = 0.48$) supporting the additive mortality hypothesis.

Discussion

Through a mixture of hunting, poaching, vehicle accidents, and depredation complaints, human caused mortality shaped the survival of mountain lions in our study area. Hunting was the leading cause of mortality, with all animals having a 22% probability of being harvested in any given year. Survival modeling showed that the Pop_3 and Pop_4 models, both based on quota levels and protection from hunting, best fit the survival experience of all ages of mountain lions on the landscape, while the model that best fit the quotas set by MFWP, the PopMan model, was the 7th best model. The Pop_3 model demonstrates the distinct difference between the hunting pressures of the Garnet study area and remainder of the Blackfoot following the restriction of hunting in 2001. The relatively poor performance of the PopMan model, suggests that there was no significant difference in survival between model, or population, segments. We interpret this to show that the incremental reductions in quotas following 2000 did not result in significant differences in population-level survival rates. Only after female quotas were set to 0 in 2005 outside the Garnet, was survival different than the previous years, as suggested by the Pop_4 model.

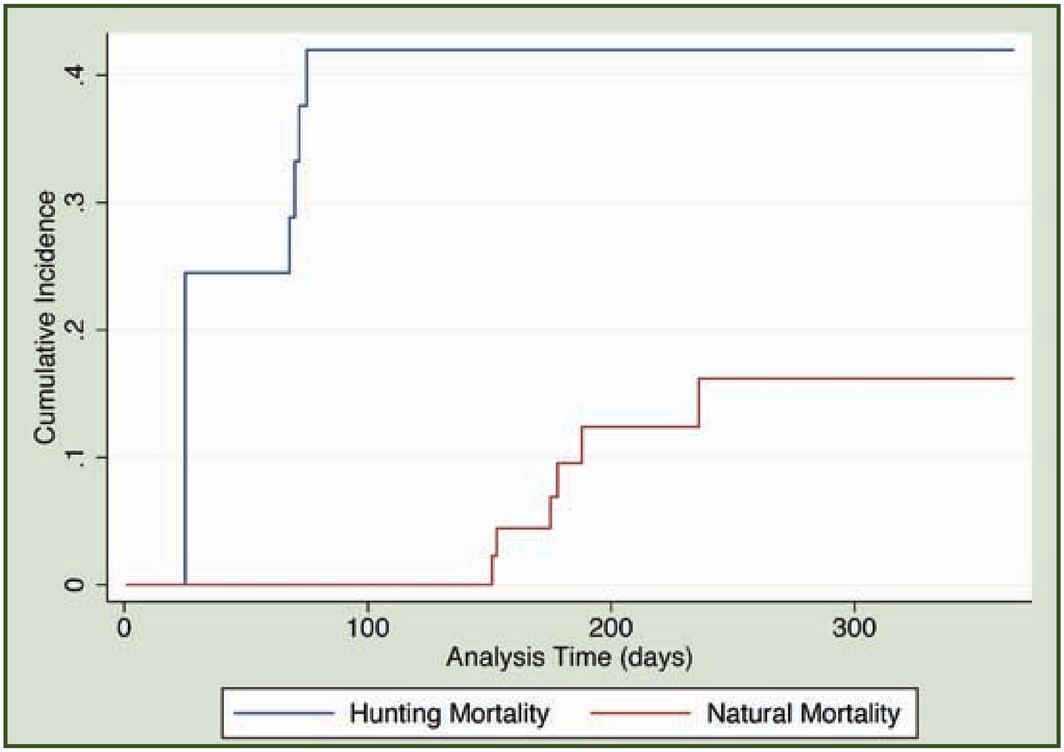


Figure 4.19. Kitten cumulative incidence functions (annual cause-specific mortality) comparing hunting mortality (starvation following orphaning) prior to protection of the Garnet study area, and natural mortality (infanticide) following.

The compensatory hunting mortality hypothesis suggests that harvest reduces the probability of animals experiencing other sources of mortality, thus allowing survival rates to remain relatively constant. We found a linear decrease in total survival of adult and juveniles with increased hunting mortality. We also found that mortality due to all other causes (i.e. illegal, natural, depredation, vehicle and unknown) was actually lower in the non-hunted population when compared to the hunted population. Both of these findings support the additive hunting mortality hypothesis.

We found an essentially equal number of kitten mortalities due to the direct effects of hunting through abandonment and natural mortality following closure to hunting of the Garnet. However, due to the timing of hunting mortalities, early in the biological year, and the longer period of monitoring time and sample size following closure of the Garnet, estimated mortality rates due to hunting were significantly higher. This suggests that the main influence of hunting on kitten survival is starvation due to abandonment, not infanticide, and that increases in natural mortality do not compensate for hunting losses of kittens.

Our results regarding the additive nature of hunting mortality in mountain lion populations, build on the previous results of Cooley et al. (2009). The additive effects of harvest, not only on adults but also through the orphaning of kittens, suggests that hunting, especially of adult females, shapes survival in hunted populations and has the potential to quickly reduce population levels. As such, wildlife managers have the ability to directly limit mountain lion population growth through the use of human harvest.

Logan and Sweanor (2001) described the "sledgehammer approach", where hunting quotas are set mainly by the previous season's hunter success rate. As success rates decline, quotas may be reduced, however due to a lack of inexpensive and reliable methods for tracking populations

Human caused mortality shaped the survival of mountain lions in our study area.

even reduced quotas may not match existing population levels leading to further declines. Our survival modeling suggested that incremental reductions in quotas outside the protected Garnet study area did not result in significant increases in adult survival until female quotas were reduced to 0.

Hounds Sugar and Stash treeing adult male M92. (Photo courtesy of Melanie Trapkus)

Houndsmen Tony Knuchel with Cooter, Sanford Strout with Stash and Grover Hedrick with Sugar. (Photo courtesy of Melanie Trapkus)

Grover Hedrick with Sugar and Raven. (Photo courtesy of Melanie Trapkus)

Rose treeing a lion. (Photo courtesy of Grover Hedrick)

Tony Knuchel with Cooter and Buck. (Photo courtesy of Melanie Trapkus)

Bob Wiesner with Pete and Radar. (Photo courtesy of Bob Wiesner)

Darting guns on dogbox with Sugar and Raven. (Photo courtesy of Melanie Trapkus)

Grover Hedrick on snowmobile with dogbox. (Photo courtesy of Melanie Trapkus)

POPULATION MODELING AND GROWTH - SECTION 5

INTRODUCTION

Hunting can have dramatic effects on mountain lion survival (see Section 4). However, ultimately managers need to understand how hunting and survival in turn affect population dynamics.

Demographic analysis through construction of matrix population models is a widely used tool for exploring the relationship of various population parameters, or vital rates, and population growth (Getz and Haight 1989, Caswell 2001). Sensitivity and elasticity analysis are two related methods used to quantify the relative contribution of each matrix parameter or vital rate (i.e. female survival or maternity) to population growth (Mills 2007). Ecologists have used matrix models and the quantifiable properties of sensitivity and elasticity to mathematically describe the consequences of varying vital rates of several species with differing life strategies. In long-lived vertebrates, and other k-selected species, adult female survival normally has the highest demographic elasticity (Gaillard et al. 1998, 2000); meaning that small changes in female survival will have the largest proportional change on population growth rate. This makes adult female survival the most targeted parameter for managing the size of populations (i.e. limited female harvest might be used to achieve population increases while liberal female harvests might be used to achieve population reductions).

Uncollared adult male treed near Clearwater Lake north of Seeley Lake.
(Photo courtesy of Grover Hedrick)

Evolution theory suggests that natural selection will favor low levels of variation in population parameters that contribute most to population growth (Pfister 1998). If k-selected species have adapted life strategies where the most important vital rates have the lowest degree of variability, hunting may disrupt this adaptive strategy by increasing the variance of, for example, female survival.

Ultimately managers need to understand how hunting and survival in turn affect population dynamics.

Although sensitivity or elasticity analysis will reveal which vital rates have the greatest effect on population growth, those same vital rates may have such low natural variability that functionally they account for little variation in population growth between years. Wisdom et al. (2000) developed an extension of elasticity analysis called life-stage simulation analysis (LSA), which measures the effects of annual variance in vital rates on population growth. To date this approach has been used to identify vital rates that may be most efficiently targeted for species management (Johnson et al. 2010). For instance adult female elk survival has a much greater elasticity than calf survival. However, the greater natural variability in annual calf survival explains 75% of the variation in population growth between years suggesting management actions centered on increasing calf survival may be more effective than those focused on adult survival (Raithel et al. 2007). Here we use LSA to quantify how harvest affects the natural variability of vital rates, and how those changes are reflected in annual population growth.

Seven and a half month old male kitten M98. (Photo courtesy of Melanie Trapkus)

We developed stage-structured matrix models parameterized using demographic data discussed in the previous sections, including population structure. Our goal was first to model population growth for comparison to population indices (see Section 6), and secondly to analyze how human harvest influenced annual population growth using sensitivity and life-stage simulation analyses.

We developed stage-structured matrix models parameterized using demographic data discussed in the previous sections, including population structure.

METHODS

We constructed, stage based, dual-sex Leslie matrix models (Leslie 1945) in MATLAB ® (The MathWorks, Natick MA) based on the two top survival models from section 4 (Pop_3 and Pop_4) using the calculated survival and fecundity parameters described below. Stochastic growth rates and associated standard deviations were calculated by running 10000, 2 to 6 year iterations (dependent on population segment, see Figures 4.5 and 4.6) with the inclusion of annual process variance for each vital rate (White 2000). We tested for the effect of dispersal from the Garnet study area to the remainder of the Blackfoot drainage by comparing stochastic population growth rates, with and without dispersal, using randomization tests (Caswell 2001).

Survival

We used age and sex specific survival rates previously discussed (see Section 4, and Tables 4.6 and 4.7) calculated using the Nelson-Aalen estimator. We calculated variance of the Nelson-Aalen survival estimator following Anderson et al. (1997):

$$Var\left(\hat{S}(t)\right)=\left(\hat{S}(t)\right)^{2}V^{2}(t)$$

(equation 5.1)

and

$$V^{2}(t)=\sum_{\{i:t_i<t\}}\frac{d_i\left(r_i-d_i\right)}{r_i^{3}}$$

(equation 5.2)

Where $\hat{S}(t)$ is the survival estimate to time t, d_i is the number of deaths at time t_i, and r is the number at risk at time t_i. We then used White's method to remove sampling variance from annual estimations of survival variance, and included this value of process variance in a beta distributed variance vector in each matrix model (Morris and Doak 2002).

Maternity and Fecundity

We assumed that females did not breed until becoming subadults (>24months, see Section 3) (Root 2004, Robinson et al. 2008). We also assumed an equal ratio of male and female kittens (total maturnity divided equally between sexes) (Logan and Sweanor 2001). Variance in maternity was modeled using a stretched beta distribution with a maximum value of 2.5 annually, or maximum litter size of 5 every two years (Morris and Doak 2002). Mountain lions give birth year-round and therefore should be modeled as a "birth flow" population (Caswell 2001). In birth flow populations fecundity (F) becomes the product of maternity and survival of both reproductive females and kittens to approximately the middle of the census period or

$$F = \sqrt{S_a} * \sqrt{S_k} * M_a \qquad \text{(equation 5.3)}$$

where S_a and S_k are adult and kitten survival respectively, and M_a is annual maternity (Morris and Doak 2002).

Dispersal

We calculated a dispersal rate based on the number of independent juveniles in each year that moved between the Garnet study area and the remainder of the Blackfoot drainage compared to the number monitored. In this sense, our modeling definition of dispersal does not match the more traditional definition (reported in Section 3), where juveniles that establish home ranges with >5% overlap of their maternal home range are considered to be philopatric rather than dispersers (Logan and Sweanor 2001). Our model assumes a closed system consisting only of two populations, the Garnet study area and the remainder of the Blackfoot watershed. Therefore, for parameterization of our population models, it was possible for an animal to establish a home range adjacent or overlapping with their mother's (philopatry) but still be classified as a disperser if their new home range was primarily outside their maternal area (the Garnet area or the remainder of the drainage). Juveniles that dispersed out of the Blackfoot watershed completely were not considered as dispersers as they were effectively lost to this system/population model and were censored.

We calculated a dispersal rate based on the number of independent juveniles in each year.

Initial Abundance and Density Dependence

Initial 1998 abundances were set at 37 animals for the Garnet study area based on a minimum population estimate calculated by back calculation of known-aged lions (Section 3), and 283 individuals in the remainder of the Blackfoot drainage, extrapolating a similar density (4.0 mountain lions/100km^2) to the remainder of the

Subadult radio-collared male M75 still in his natal home range at 21 months of age. (Photo courtesy of Melanie Trapkus)

Biologists Rich DeSimone and Vickie Edwards fitting an adult radio-collar on a 10 month old female F96, also in attendance MFWP Wildlife Manager John Firebaugh, MFWP Commissioner Vic Workman and landowners Stacey and Sheila Manley. (Photo courtesy of Melanie Trapkus)

watershed. All models were started in 1998 at a stable age distribution, then using the mean modeled age distribution for further projections. For instance the pop_3 model was started in 1998 with a stable age distribution and run for 3 years, when survival rates changed/diverged between the Garnet and remainder of the Blackfoot. Then a second run covering the period 2001 to 2007 was started based on the age distribution outputs from the 1998 to 2000 model. Ceiling density dependence was added to stochastic models and assumed to affect survival of subadults and adults (>24 months) only (Root 2004). Applying ceiling density to independent animals only simulates territoriality. Carrying capacity was set at 27 adults for the Garnet study area and 210 adults for the remainder of the Blackfoot drainage based on an average density of 3 adults per 100 km^2. This is a liberal estimate of maximum adult density, commensurate with observed levels of 2.92 /100km^2 in Wyoming (Anderson and Lindzey 2005) and 2.58/100km^2 in northeastern Washington (Robinson et al. 2008).

We tested the effect of each population parameter on population growth rate through perturbation.

Sensitivity and Life-Stage Simulation Analysis

We tested the effect of each population parameter on population growth rate through perturbation. The sensitivity of lambda to each vital rate (i.e. survival, maternity, emigration, etc.) was calculated by individually reducing each by 0.10 and recalculating lambda from each matrix (Caswell 2001). We conducted a life stage simulation analysis (LSA) to quantify the effects of variance on the population growth within the Garnet study area separately during the hunted period (1998 to 2000), and the non-hunted period (2001 to 2006). We compared the R^2 values for each vital rate for each period (Wisdom et al. 2000), essentially comparing the proportion of variation in population growth explained by the variation in that vital rate. Sensitivity analysis was conducted using the Pop_3 and Pop_4 models. As we were only interested in the effect of harvest on vital rate variability and population growth, life-stage simulation analysis was conducted on only the Garnet portion of the Pop_3 model pre- and post-harvest.

Finally, given the results of our sensitivity and LSA analysis, we constructed a deterministic population model to graphically quantify how varying levels of maternity, as well as female kitten and adult survival combine to affect population growth. We fixed all male survival rates as well as juvenile female survival at the average levels observed for the entire study population and we varied kitten and adult female survival by increments of 0.05 ranging from 0.01 to 1.0. The probability of a kitten surviving to become a juvenile was the combined function of kitten and adult survival (i.e. kitten survival x adult survival) to mimic the affect of kitten abandonment following an adult's death. Fecundity levels were modeled as in the other population models. We graphed growth rates using the above survival and fecundity rates at 3 levels of maternity, 1.08, 1.29, and 1.40; maternity during the hunting period, mean maternity across the study period, and maternity during the non-hunting period respectively (see Section 3).

Results

Survival

Survival estimates for each sex and age class, in each population segment were presented previously in section 4.

Maternity and Fecundity

Mean maternity for the Garnet study area was 1.29 kittens per female per year. Birth flow, sex specific fecundity rates used in population model segments ranged from 0.42 to 0.59, varying with each segment's kitten and adult female survival.

Dispersal

Of 15 kittens collared in the Blackfoot watershed and 64 collared in the Garnet study area, a total of 47 were monitored until independence from their mothers. One female and 6 males dispersed out of the watershed completely and were censored from dispersal rate calculations. Mean age of dispersal was 15 months (n = 33, range 11 - 23 months). Dispersal rates of juveniles from the refuge to the hunted area were 0 prior to the cessation of hunting, but increased to 0.82 ± 0.19 per year for females and 0.71 ± 0.39 per year for males once the area was closed to hunting. No radio collared juveniles emigrated into the Garnet study area from the remainder of the Blackfoot watershed, where hunting was allowed, although low juvenile survival (see Tables 4.6 and 4.7) reduced the number of independent juveniles in our sample to 4, all of which remained in the hunted Blackfoot area.

Population Growth

Our population models suggest that the mountain lion population in the Blackfoot watershed was declining by approximately 8 - 12% per year between 1998 and 2000 (Pop_3 λ = 0.88 ± 0.08, Pop_4 λ = 0.92 ± 0.10). With the cessation of hunting in the Garnet study area in 2001, the Pop_3 model predicts recovery beginning immediately with the population growing at approximately 6% annually (λ = 1.06±0.05) (Table 5.1). The Pop_4 models suggests that mountain lion numbers in the watershed were slightly declining or stable (λ = 0.98 ± 0.09) between 2001 and 2004, before climbing rapidly following reductions in quotas outside the Garnet in 2005 (λ = 1.15 ± 0.09 (Table 5.2). Both models predict a watershed wide population level at the end of the study, in January 2007, very near initial 1998 levels (Figure 5.1). Both models also predict final

Dispersal rates of juveniles from the refuge to the hunted area were 0 prior to the cessation of hunting.

Table 5.1. Modeled population growth rate (± SD) based on Pop_3 model.

	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet Study Area	λ = 0.8709 ± 0.08			λ = 1.0119 ± 0.05					
Blackfoot outside Garnet Study Area	λ = 0.8816 ± 0.08			λ = 1.0617 ± 0.05					
Combined Watershed Population	**λ = 0.8822 ± 0.08**			**λ = 1.0581 ± 0.05**					

Table 5.2. Modeled population growth rate (± SD) based on Pop_4 model.

	1998 1999 2000	2001 2002 2003 2004	2005 2006
Garnet Study Area	λ = 0.9535 ±0.10	λ = 0.9584 ± 0.06	λ = 0.9965 ±0.08
Blackfoot outside Garnet Study Area	λ = 0.9112 ± 0.11	λ =0.9807 ± 0.10	λ = 1.1721 ±0.09
Combined Watershed	***λ = 0.8822 ± 0.08***	***λ = 1.0581 ± 0.05***	***λ = 1.1547 ± 0.09***

Dispersal from the protected Garnet study area significantly reduced that population segment's growth.

densities in the Garnet study area of approximately 26 individuals, 11 fewer than at the start of the study. The trend in watershed wide estimates from both modeled populations matches the minimum estimate for the Garnet based on backdating (Figure 5.1), however both models predict a slower recovery within the Garnet study area than the minimum estimate for the number of lions based on backdating (Figure 5.2).

Dispersal from the protected Garnet study area significantly reduced that population segment's growth, while having a small effect on the hunted area of the Blackfoot and the watershed as a whole. Population growth in the Garnet with dispersal to the hunted area was 1.01 ±0.05. Without dispersal the Garnet population would have grown at a higher annual rate of 1.17±0.03 ($\theta = -0.16$, $P = 0.12$). Dispersal increased the mean population growth rate of the remainder of the Blackfoot area by 3% (from 1.03±0.05 to 1.06±0.05) although this increase was not statistically significant ($\theta = 0.02$, $P = 0.40$).

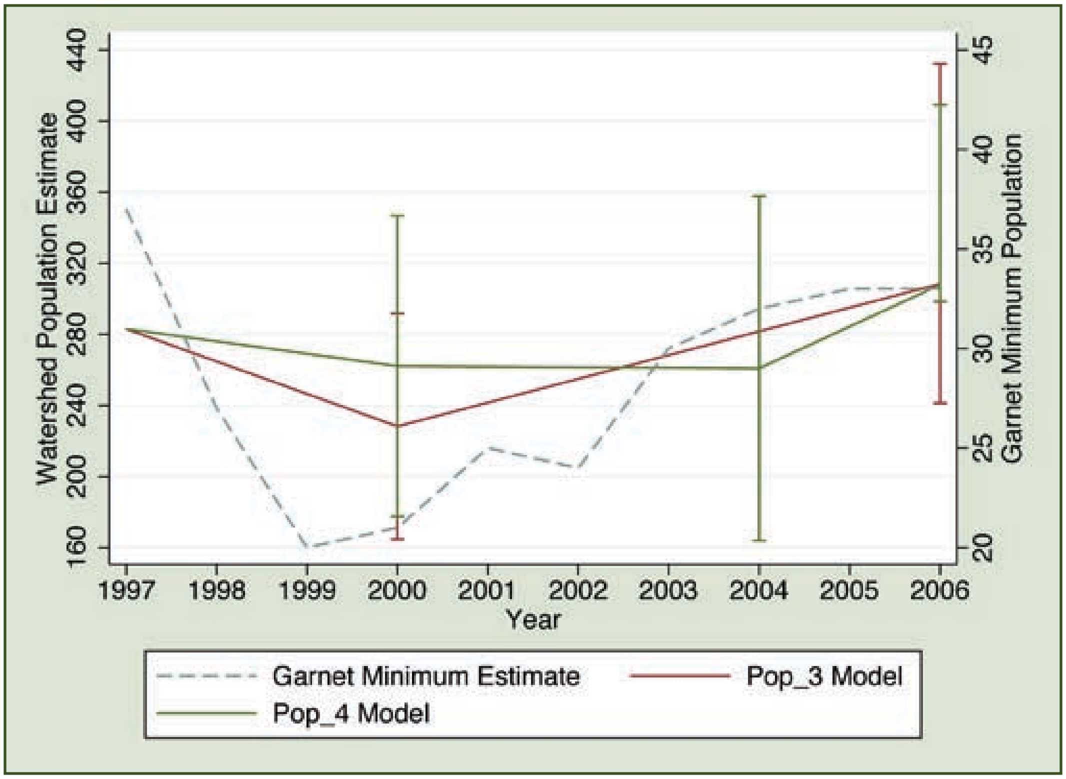


Figure 5.1. Projected population levels (± 1 SD) for the entire Blackfoot watershed, including Garnet study area, based on top population models (pop_3 and pop_4, see table 4.3). Minimum population estimate for the Garnet study area, based on backdating known aged animals, included for comparison.

Sensitivity and Life Stage Analysis

The growth rate of the Blackfoot watershed mountain lion population was most sensitive to changes in adult female survival followed by other measures of female survival (either juvenile or kitten) and maternity (Figure 5.3). Negative sensitivities of dispersal from the Garnet to the hunted area of the watershed following 2001 attest to the lower survival probability of adults in the hunted area compared to the protected Garnet. Life-stage simulation analysis showed that hunting almost doubled the importance of adult female survival to population growth, while reducing the significance of kitten survival and maternity (Figure 5.4). Combined, adult female survival, female kitten survival, and maternity account for 92% and 57% of the variability in annual population growth of non-hunted and hunted populations respectively. The combined effects of adult female and kitten survival on population growth at three levels of maternity are shown in Figure 5.5. In general adult female survival levels below 0.80 should lead to declining population levels.

DISCUSSION

Population models that incorporate our top survival models result in similar predicted population level outcomes. Our models suggest that the mountain lion population in the greater Blackfoot watershed was declining annually between 8 and 12% prior to the protection of the Garnet study area in 2001, but recovered to near 1998 levels by the end of the study in 2007 due to the protection of the Garnet area, dispersal out of protected Garnet, and reduced quotas in the remainder of the watershed beginning in 2004. The range in the level of decline

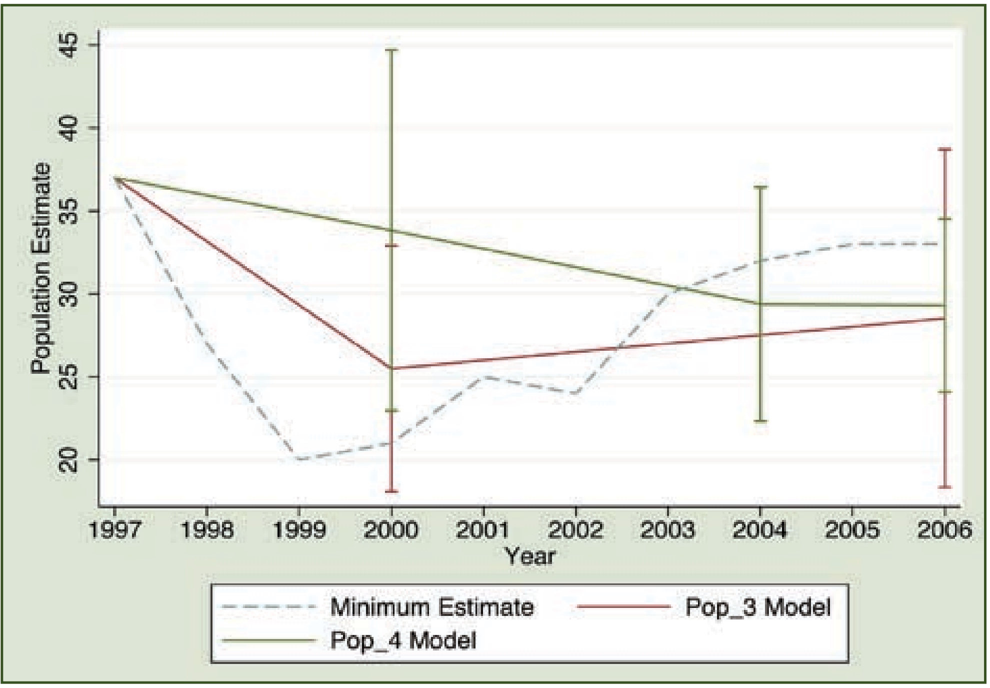


Figure 5.2. Projected population levels (± 1 SD) for the Garnet study area based on top population models (pop_3 and pop_4, see table 4.3). Minimum population estimate for the Garnet study area, based on backdating known aged animals, included for comparison.

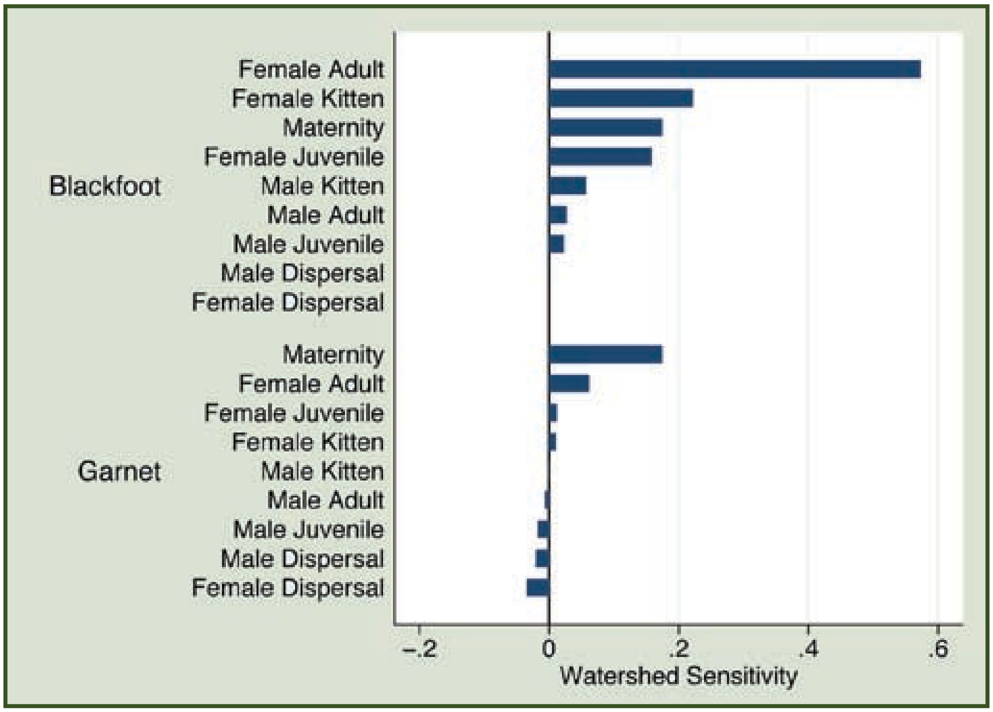


Figure 5.3. Sensitivities of mountain lion population growth to matrix vital rates of the Pop_3 model 2001 - 2006. Maternity sensitivity is for both the Garnet and Blackfoot hunted area subpopulations (for ease of interpretation, only sensitivities of the entire watershed population based on the Pop_3 model are presented, although the sensitivities for all population segments from other population models were similar).

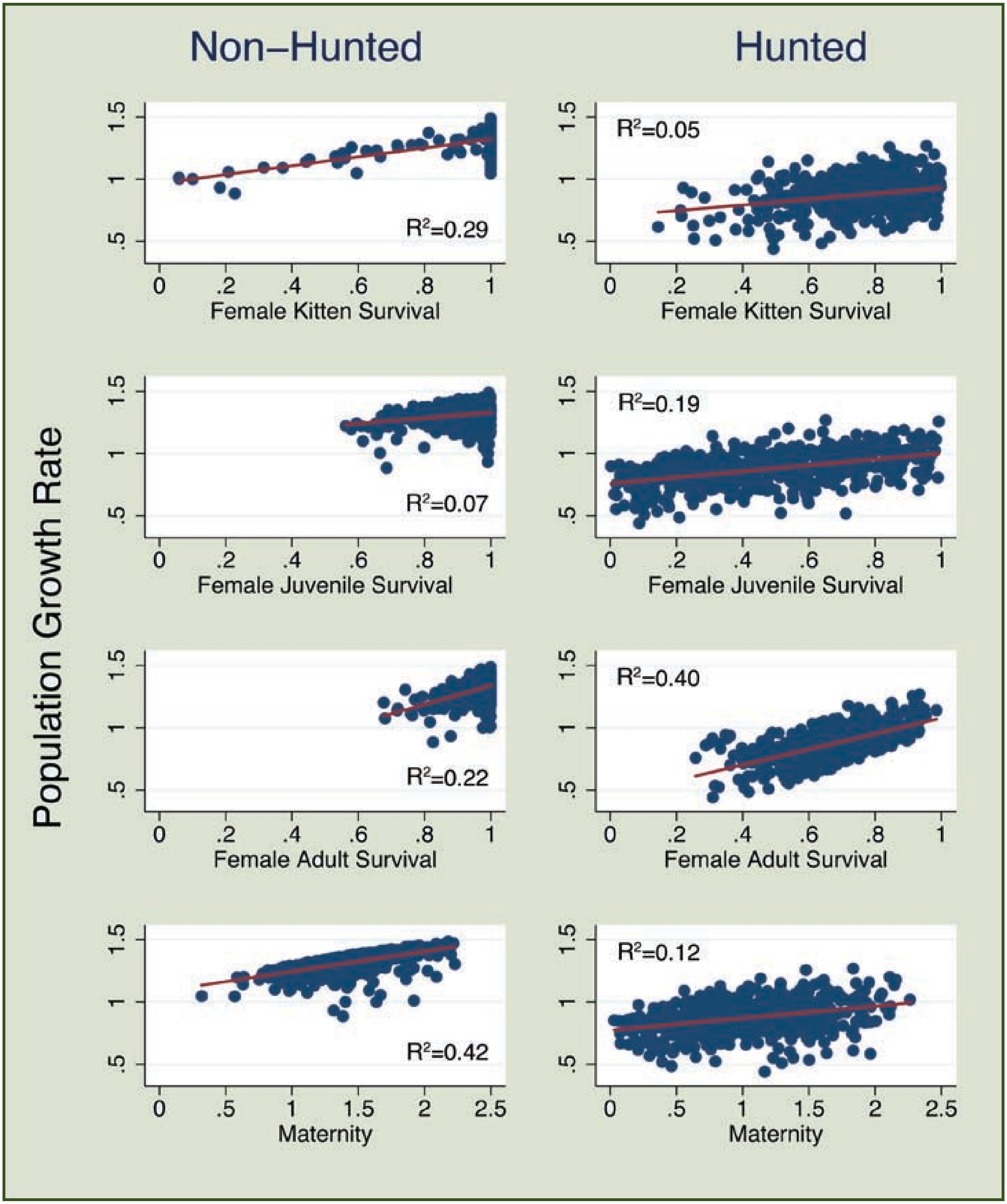


Figure 5.4. Life–stage simulation analysis (LSA) for the Garnet study area during the hunted and protected periods. The R^2 value describes the proportion of the variation in population growth explained by variation in the vital rate. Values for males omitted as their survival rates and associated variances had little effect on population growth.

predicted by the two models is the result of slightly different estimated survival rates for the various model segments represented in the top survival models. The Pop_4 model does not show as much decline by the end of 2000 because calculated segment 2 survival rates include higher survival levels outside the Garnet area in the later years of the segment. Segment 1 of the Pop_3 model has the lowest calculated survival rates and therefore the lowest predicted growth rates. How quickly, and to what level our population models predict that the populations recovered is influenced by the same differences in survival represented by the different survival models.

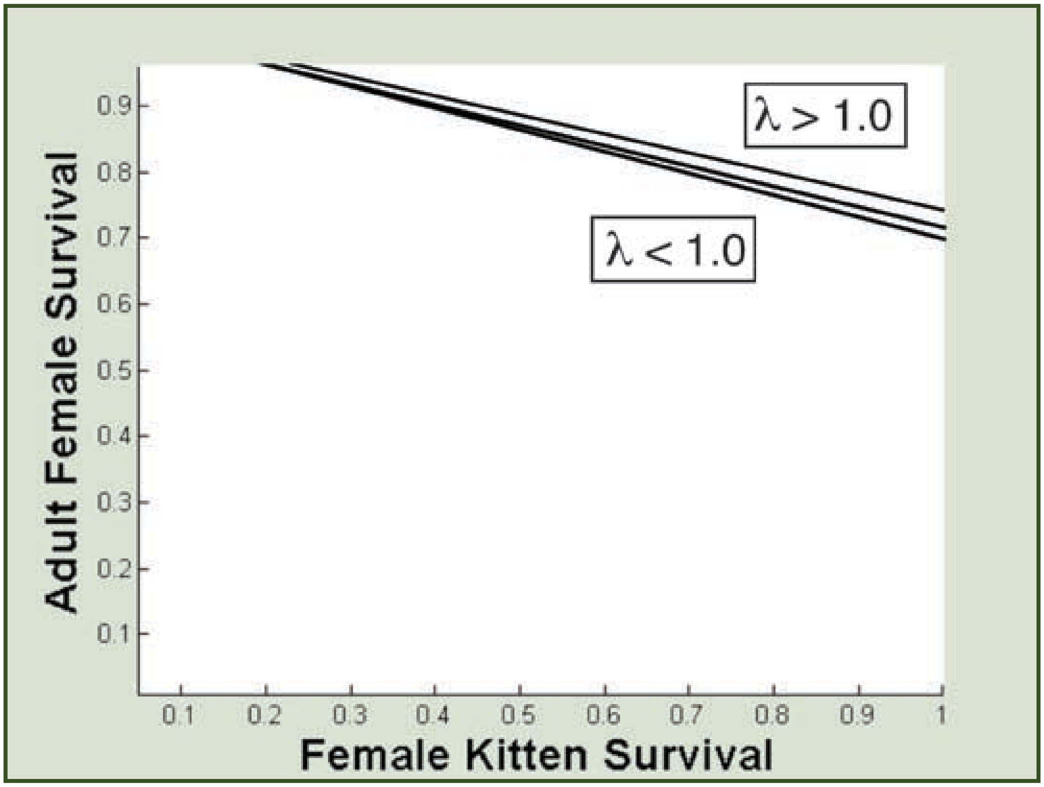


Figure 5.5. The relationship of female kitten survival, adult female survival, and population growth at maternity rates of 1.08 (top), 1.29 (middle) and 1.4 (bottom). Areas above the lines represent possible lambda values greater than 1.0 while areas below represent survival levels which may lead to a decline in population.

Our sensitivity analyses showed that second in importance to female survival rates in influencing population growth rates was maternity. It is important to stress that sensitivity analysis does not take into account annual variability as the life-stage simulation analysis does. Although maternity rate was held constant for all models at 1.29 kittens per female per year, fecundity is a function of maternity, adult female and kitten survival. Differences in fecundity also partially explain the different performance of each model segment.

Sensitivity analysis also showed that dispersal of both juvenile males and females from the protected Garnet into the hunted Blackfoot watershed had a strong negative effect on Garnet population growth, and a weak negative effect on growth in the watershed as a whole.

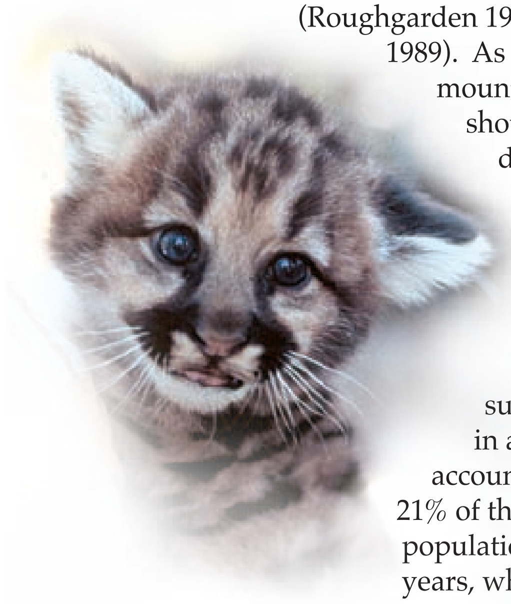
Although real emigration from the Garnet to the remainder of the Blackfoot likely had a small positive effect on the watershed population, sensitivity analysis only takes into account the structure of the matrix model. In this sense animals emigrating out of an area, especially females, are essentially lost to that population, resulting in a negative sensitivity (i.e. negative sensitivity for the Garnet). The negative sensitivity of female dispersal from the Garnet to the Blackfoot watershed population as a whole is due to the lower survival rates in the unprotected portion of the Blackfoot. In essence the matrix model is suggesting that juveniles would be better off remaining where their probability of survival and reproduction were higher, inside the Garnet.

Further simulation, varying dispersal

Dispersal of both juvenile males and females from the protected Garnet into the hunted Blackfoot watershed had a strong negative effect on Garnet population growth.

and harvest levels, are required to estimate the population level effect of protecting 12% of the landscape.. However, our initial analysis suggests that an area as small as the Garnet (915 km^2) can act as a viable reserve with increased survival rates and an ability to produce emigrants to other, more heavily hunted areas. Appropriate refuge size will ultimately depend on relative population densities, and harvest levels.

Adult female survival rates greater than 0.75, and likely closer to 0.85 are required for population growth.



5 week old kitten of radio-collared female F19. (Photo courtesy of Milo Burcham)

Our life-stage simulation analysis clearly demonstrates the effect of hunting on the normal population dynamics of mountain lions. Evolutionary theory points to survival and fecundity as defining fitness (Roughgarden 1979, Hartle and Clark 1989). As a long-lived species, mountain lion populations should show the lowest degree of variability in the vital rate that contributes most to fitness, namely adult survival. In our non-hunted population this hypothesis is supported, variability in adult survival is low accounting for approximately 21% of the variation in population growth between years, while reproduction (kitten survival and maternity) accounted for approximately 70%. Hunting reversed this adaptive strategy shifting the reliance of population growth towards adult survival, now 45% of the variation in growth, and away from reproduction (16%). In general we found little effect of male survival on population growth. In the non-hunted segment of our population, male survival accounted for less than 1% of the variability in annual population growth; this level increased to 5% in the hunted population.

By combining the three most important vital rates to population growth (adult female survival, female kitten survival, and maternity) in a deterministic matrix model, we showed that adult female survival rates greater than 0.75, and likely closer to 0.85 (depending on kitten survival) are required for population growth. Adult female mortality rates of approximately 0.20 may be required for population reduction. Lambert et al (2006) modeled broad mountain lion population declines in British Columbia, Washington, and Idaho with adult female survival rates of 0.77.

It is important to note that our population models assumed a closed system consisting of only two populations, the Garnet and the remainder of the Blackfoot drainage. Although we found no juvenile dispersal from the Blackfoot back into the Garnet and therefore could not model the effect of immigration into the Garnet, the level of disagreement between the Pop_3 and Pop_4 models, and our minimum population estimate for the Garnet (5 animals) could be attributed to 2 litters that were born inside the Garnet and were not accounted for by our mean maternity rates or immigration from outside the Blackfoot watershed. Immigration and emigration have been shown to have dramatic affects on real population growth rates when compared to modeled rates. Accounting for immigration and emigration, Cooley et al (2009) showed real population decline (λ=0.91) in a heavily hunted area with adult female survival estimated at 0.66. Without immigration it was estimated through a similar modeling process as we used here, that population growth would have been significantly lower, 0.78. That same study, found an essentially stable real population growth rate (λ=0.98) in a lightly hunted population with adult female survival of 0.87, with emigration reducing modeled growth from 1.10.

TRACKING POPULATIONS WITH INDICES - SECTION 6

INTRODUCTION

Quantifying mountain lion population size is a notoriously difficult endeavor. Lions, by their nature, are not well suited to most methods of measuring abundance. Their cryptic coloration, use of dense foliage for cover, and solitary nature hamper most census techniques. To date, intensive collaring programs have proven best for establishing an absolute, or at least minimum, estimate of abundance and population growth (e.g. Spreadbury et al. 1996, Logan and Sweanor 2001, Stoner et al. 2006). This level of monitoring however is difficult, requires a high level of personnel hours, and can be extremely expensive. Thus despite their importance as a game species and public concern regarding mountain lion populations, most jurisdictions resort to the use of population indices to gauge population levels or trends (e.g. Oregon Department of Fish and Wildlife 2006).

An index is generally considered any count of animals, or their sign, that is directly tied to their true abundance, without actually estimating density. Common examples include pellet counts, track surveys, harvest data, and questionnaires of wildlife sightings (Mills 2007). It is assumed that a simple linear relationship exists between the index value and true population density (Eberhardt and Simmons 1987, Bart et al. 2004).

The first published index of mountain lion abundance was published in 1954. Johnson and Couch (1954) proposed a formula based on the assumption that the true, pre-harvest population must be approximately 3 times the number harvested, as it takes 2 mountain lions to produce the one killed. Since that time, authors have tried to match mountain lion populations to livestock damage and human safety complaints (Keister and Van Dyke 2002), harvest characteristics (Anderson and Lindzey 2005), and perhaps most prevalently track surveys (Van Sickle and Lindzey 1991, Van Sickle and Lindzey 1992, Beier and Cunningham 1996).

Quantifying mountain lion population size is a notoriously difficult endeavor.

Mountain lion, human and vehicle tracks on a logging road in fresh snow. (Photo courtesy of Hugh Robinson)

We measured reliability of collected indices in three ways; the precision of the index, the relationship between the index and an estimated abundance, and the power of the index to detect changes in population size.

Mountain lion track surveys have been considered a practical method for detecting and monitoring lion populations because they are relatively inexpensive to conduct over large areas and tracks are often easier to 'capture' than sightings, photographs, or actual lions (Beier and Cunningham 1996). Presence can be relatively simple to document when tracking surveys are conducted by competent trackers (Van Dyke et al. 1986). However, they have been shown to lack power to detect all but large (i.e. >50%) changes in population level (Van Sickle and Lindzey 1992, Beier and Cunningham 1996, Choate et al. 2006).

The ability to validate the accuracy or precision of an index is limited when studies are conducted where actual animal densities are not known. Eberhardt and Simmons (1987) proposed calibrating indices through double sampling, where index data are converted to a true measure of abundance through comparison to a second or reference census. Our goal in this chapter was to test the reliability of some popular indices of mountain lion abundance. We tested for agreement between our minimum population estimate (Section 3), two modeled population estimates (Section 5) and several commonly collected population indices, treating our population models as a reference method (Caley and Morley 2002, Marchandeau et al. 2006).

The challenge of accurately identifying tracks is illustrated by this photo - what appear to be a mountain lion female and kitten is actually a Canada lynx and bobcat track. (Photo courtesy of Grover Hedrick)

METHODS

We measured reliability of collected indices in three ways; the precision of the index, the relationship between the index and an estimated abundance, and the power of the index to detect changes in population size (Marchandeau et al. 2006). We estimated the precision of each index using the coefficient of variation across all years a particular index was collected (Thompson et al. 1998). We conducted a simple linear regression between each index and the modeled population estimate or the minimum number of lions in the Garnet, where the index was the dependent variable and our modeled or minimum population estimate independent. In this case we were interested in the relationship between the modeled population level, which we treated as true, and the index, as opposed to calibrating an index in which case the dependent and independent variables would be reversed. Finally, we used program TRENDS (Gerrodette 1993) to estimate the statistical power of each index. Tests were based on exponential change (i.e. an equal proportional change each year, for example 25%/year), equal intervals between sampling occasions, and coefficients of variation that changed with abundance proportional to $1/\sqrt{abundance}$ (Gerrodette 1993).

Some indices were collected and therefore examined at different scales. For instance track surveys were conducted in the Garnet study area only, thus limiting their comparison to our minimum population estimates (also calculated only within the Garnet) and the Garnet specific predictions of our two top population models from section 5. All other indices, (i.e. harvest characteristics, hunter effort, and public observation data) were collected for the entire Blackfoot watershed facilitating their comparison to our watershed wide population models.

Age and Sex Ratio of Harvested Lions

In Montana, successful mountain lion hunters are required to present the hide and skull for inspection within 10 days of harvest. At that time, sex of the animal is recorded and a tooth is collected for aging (Matson Lab, Milltown MT). We used sex and age data collected from these mandatory checks to test the ratio of females to males in the harvest, and mean age of harvested animals as indices of population trend, against the pop_3 and pop_4 modeled population estimates for the Blackfoot watershed.

Snow track Surveys

Winter snow-track surveys were conducted in the Garnet study area from November 3, 2000 to March 20, 2005. Eleven snow-track survey routes totaling 250 km (155 miles) were established and were designed to representatively sample the various habitat types, cover types and other environmental features of the Garnet (Figure 6.1). All snow-track routes were on established roads and trails and were surveyed by snowmobile.

Snow-track routes were inventoried 3 to 12 times each year. For each mountain lion track or track-set encountered, the location and habitat description was recorded as well as the age of the track, the days since last snow and whether the track was made before or after the last snow. At each lion track or group of tracks, measurements of pad width, track width and stride length were recorded. Tracks associated with groups of lions traveling together were analyzed as both as individual tracks as well as single track-sets or 'incidents' (Van Sickle and Lindzey 1991). Lion tracks were not recorded if they were observed within 3 snowmobile lengths of previous tracks, or had similar measurements as other track sets recorded in the immediate vicinity (i.e. pad, track width and stride length). From these data, we estimated the number of lion tracks per mile and the number of groups of tracks per mile as potential indices of lion abundance in the Garnet study area. We compared these indices to the minimum number of lions present in the Garnet study area as well as modeled population estimates for the Garnet study area only.

Winter snow-track surveys were conducted in the Garnet study area from November 3, 2000 to March 20, 2005.

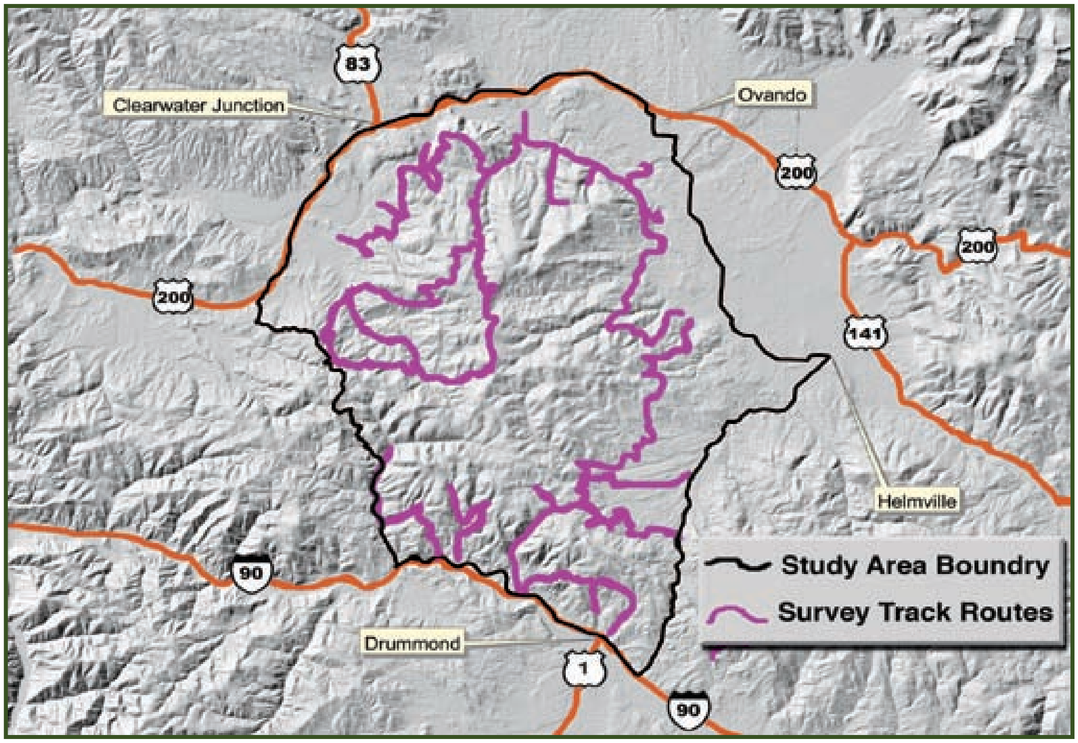


Figure 6.1. Snow-track survey routes within the Garnet study area, western Montana, November 2000 to March 2005.

Resident deer and mountain lion license holders were surveyed to collect data on the number of hunters that observed mountain lions.

Public Observations and Hunter Effort

We collected data on public observations and hunter effort, essentially catch per unit effort index data in three ways; through stratified statewide phone surveys, by interviewing houndsmen, and from harvest forms. Montana Fish Wildlife and Parks conduct surveys of public hunting effort, harvest, and wildlife observations annually. As a part of this project, resident deer and mountain lion license holders were surveyed to collect data on the number of hunters that observed mountain lions. These indices were all compared against modeled lion population estimates for the entire Blackfoot drainage.

Houndsmen/biologists Grover Hedrick and Stanford Strout in the northern portion of the Garnet Mountains south of Clearwater Junction on the Cap Wallace Road. (Photo courtesy of Melanie Trapkus)

From 2003 and 2008 a stratified network sample of resident deer hunters was selected annually from populations defined by each type of deer hunting license sold during those years (Gude et al. 2006). Each year approximately 40,000-50,000 resident deer license holders were sampled depending on the hunting regulations for that year. Selected individuals where contacted and asked a series of questions including how many days they spent hunting deer, whether or not they saw mountain lions while hunting, and if so, where the observation took place and how many lions were observed. The total number of deer hunters, deer hunter days, lions observed, and ratios based on these statistics (i.e. hunter days per mountain lion observation) were estimated annually for the Blackfoot watershed using a Horvitz-Thompson estimator based on scaled up network inclusion probabilities (Thompson 2002, Gude et al. 2006, Lohr 2009).

Mountain lion hunters were also contacted by phone. During 2001-2003, lists of lion hunters hunting with their own hounds (houndsmen) in the Blackfoot drainage were compiled. Each of these hunters was contacted by project staff. Similar to the surveys of deer hunters, houndsmen were asked how many days they hunted and how many lions they treed. During 2005 and 2008, these surveys were repeated, but an effort was made to contact each mountain lion license holder in Montana using the statewide harvest survey system. Approximately two-thirds of license holders responded to these surveys. Each of the survey efforts, 2001-2003 and 2004-2008) were used to estimate the number of lion hunter effort (i.e. days per treed lion) as an index of lion abundance in the Blackfoot drainage.

In addition to phone surveys, successful lion hunters are required to complete a mountain lion harvest form, which includes questions on the number of lions observed or treed, and number of days hunted. These data were used to estimate the number of lion hunter days per harvested lion as another potential index to lion abundance in the Blackfoot drainage.

RESULTS

Age and Sex Ratio of Harvested Lions

From 1998 to 2006 a total of 299 mountain lions (158 males and 141 females) were harvested from the Blackfoot watershed, 41 of which (18 males and 23 females) were harvested from the Garnet study area. Mean age of harvested animals was 2.88 years (2.64 male and 3.16 female). There was a female quota in all but the last two years of the study in the Blackfoot watershed. This quota was filled or exceeded in each year (i.e. 100% - 133% quota), and on average females made up 37% of the animals harvested.

We found a significant relationship between the population estimates from the pop_3 model, the percentage of the female quota filled, and the percent of females in the total harvest (Table 6.1, Figure 6.2). These same two indices performed best when compared to the other harvest-based indices (Table 6.1). We found no relationship between the pop_4 model and any of the harvest indices (Table 6.2).

The coefficient of variation for each of the indices ranged between 0.13 to and 0.53. These relatively high levels of variation reduced their ability to detect a 25% change in population to between 4 and 7 years (Table 6.3). Similarly, the level of variation in age and female harvest indices reduced the probability of detecting an annual 25% change in population to between 5 and 9% (Table 6.3).

In addition to phone surveys, successful lion hunters are required to complete a mountain lion harvest form, which includes questions on the number of lions observed or treed, and number of days hunted.

Snow Track Surveys

From 2001 to 2005 we conducted 397 track surveys, covering a total of 8,953 km (5,563 miles). An average of 79 routes, or 1790 km were sampled each year, although sampling effort declined as the study progressed. Five-hundred

Table 6.1 Regression results of mountain lion harvest characteristics, harvested age and sex ratio indices and Pop_3 model, Blackfoot watershed, western Montana 1998 to 2006.

Index	p	R^2	Beta Coef.	Obs.
% Female Quota Filled	0.05	0.55	0.0048	7
% Females in Harvest	0.01	0.58	-0.0050	9
$\bar{x}$ Female Age	0.10	0.39	-0.0166	8
Total $\bar{x}$ Age	0.54	0.05	-0.0040	9
$\bar{x}$ Male Age	0.79	0.01	0.0020	9

Table 6.2 Regression results of mountain lion harvest characteristics, harvested age and sex ratio indices and Pop_4 model, Blackfoot watershed, western Montana 1998 to 2006.

Index	p	R^2	Beta Coef.	Obs.
% Female Quota Filled	0.47	0.11	-0.0021	7
% Females in Harvest	0.42	0.09	-0.0021	9
$\bar{x}$ Female Age	0.88	0.003	0.0011	9
Total $\bar{x}$ Age	0.94	0.001	0.0006	9
$\bar{x}$ Male Age	0.94	0.001	0.0011	8

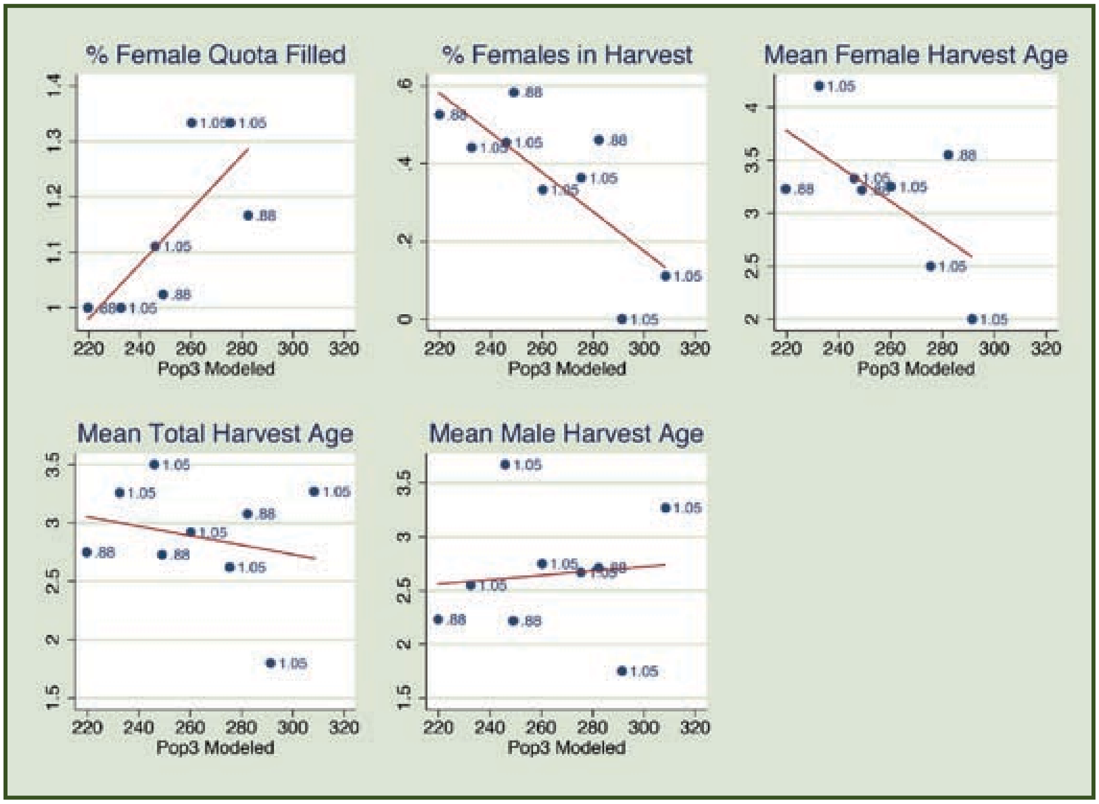


Figure 6.2. Relationship of harvest indices and modeled population estimate based on pop_3 model, 1998 to 2006 western Montana (observations are labeled with that same years calculated growth rate).

and three individual lion tracks in 370 groups were recorded (Table 6.4). We found a poor relationship between our minimum population estimate or our modeled population estimates, and the number of tracks observed each year (Table 6.5 and Figure 6.3). Based on the coefficients of variation of the track surveys (0.26 tracks/km and 0.32 groups/km), we determined that it would take between 5 and 6 years to detect a 25% change with 50% certainty (i.e. β=0.5), while the probability of detecting a 25% change in population level between seasons was 6%.

Table 6.3. Variation and power of harvest-based indices to detect a 25% change in the mountain lion population, Blackfoot watershed western Montana, 1998 to 2006.

	Male Age	Female Age	Mean Age	% Females in Harvest	% Female Quota Filled
Coefficient of Variation	0.20	0.24	0.17	0.53	0.13
Duration of study (years) to detect 25% annual change in population (β=0.5, α=0.05)	5	5	5	7	4
Probability (β) of detecting a 25% trend between years (α=0.05)	0.07	0.06	0.07	0.05	0.09

Table 6.4 Annual track survey effort and results, Garnet study area western Montana, 2001 to 2005.

Year	# of Routes Inventoried	Total Distance (km)	Tracks	Groups	Tracks/km	Groups/km
2001	114	2575	149	113	0.0578	0.0439
2002	119	2812	110	87	0.0391	0.0309
2003	65	1426	101	78	0.0708	0.0547
2004	54	1203	68	35	0.0565	0.0291
2005	45	937	75	57	0.0801	0.0608

Table 6.5 Regression results of track surveys and minimum population estimate, Pop_3 and Pop_4 population model estimates, Garnet study area, western Montana 2001 to 2005.

Index	*p*	R^2	Beta Coef.	Obs.
Tracks per mile and min. est.	0.13	0.59	0.0047	5
Groups per mile and min. est.	0.47	0.19	0.0024	5
Tracks per mile and Pop3 est.	0.25	0.39	0.0332	5
Groups per mile and Pop3 est.	0.54	0.13	0.0174	5
Tracks per mile and Pop4 est.	0.35	0.28	0.0082	5
Groups per mile and Pop4 est.	0.72	0.04	-0.0030	5

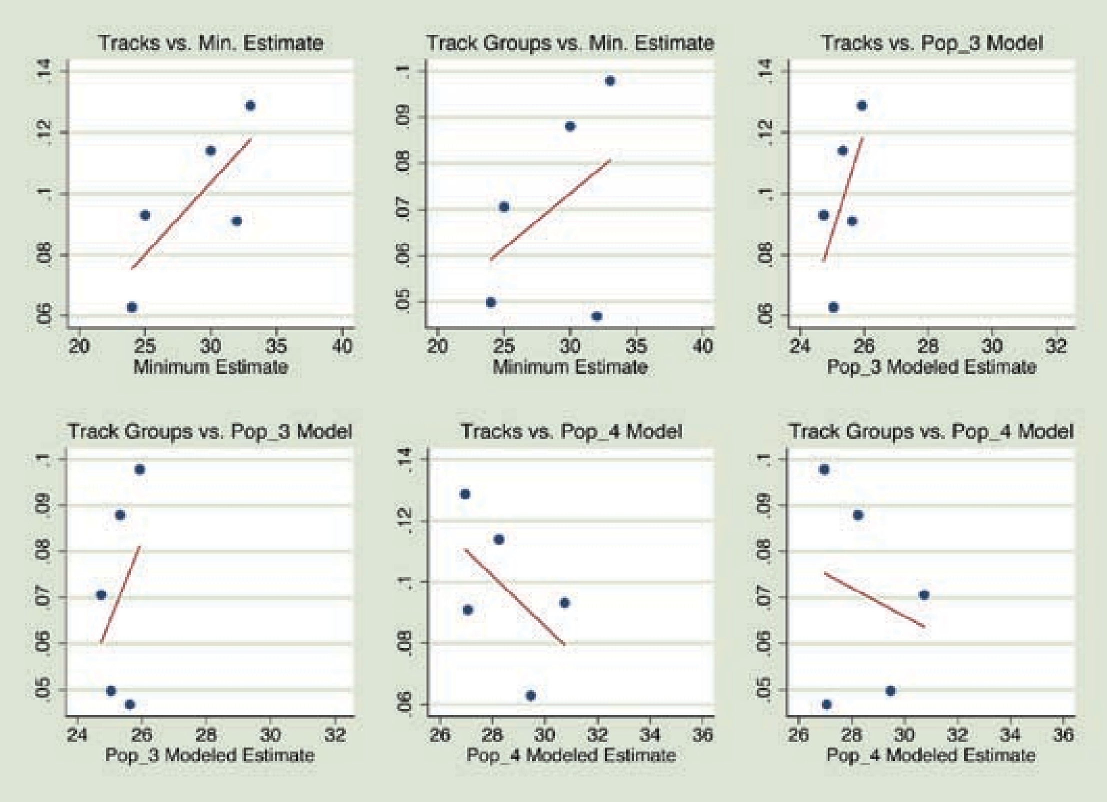


Figure 6.3 Mountain lion tracks, and groups of tracks, per mile of road surveyed as a function of modeled and estimated minimum population levels within the Garnet study area, western Montana 2001 to 2005. None of these regressions are significant.

Public Observations and Hunter Effort

We found no strong relationship between the predictions from either population model and any of the observation or effort based indices (Table 6.6, Table 6.7, Figure 6.4 and Figure 6.5). The coefficient of variation for each of the indices ranged between 0.23 to and 0.31. These levels of variation reduced their ability to have a 50% chance to detect a 25% change in population to between 7 and 8 years, while the probability of detecting a 25% change in population level between seasons was 5% (Table 6.8).

We found little agreement between most indices and any of our population estimates.

DISCUSSION

We found little agreement between most indices and any of our population estimates. Further, those indices we did find to be significantly correlated with our population estimates could be biased due to a lack of independence between the index itself and the population growth rate. We found a significant relationship between the pop_3 modeled estimates for the Blackfoot watershed, and the percent of females in the total harvest (Table 6.1 and Figure 6.2). However the independence of these two estimates should be questioned. We have shown

Table 6.6 Regression results and model selection of hunter effort indices and Pop_3 model.

Index	*p*	R^2	Beta Coef.	Obs.
% Deer hunters observing a lion	0.96	0.01	0.0005	7
Lion hunter days per treed lion	0.58	0.11	-0.0253	5
Lion hunter days per harvested lion	0.12	0.30	-0.0225	9
Deer hunter days per lion observation	0.75	0.02	0.3048	7

Table 6.7 Regression results and model selection of hunter effort indices and Pop_4 model.

Index	*p*	R^2	Beta Coef.	Obs.
% Deer hunters observing a lion	0.14	0.36	0.0196	7
Lion hunter days per treed lion	0.77	0.03	-0.0125	5
Lion hunter days per harvested lion	0.54	0.05	0.0103	9
Deer hunter days per lion observation	0.35	0.17	-1.0359	7

Table 6.8 Variation and power of hunter observation and effort based indices to detect a 25% change in the lion population, Blackfoot watershed western Montana, 1998 to 2006.

	% of deer hunters observing a lion	$\bar{x}$ deer hunter days per lion observed	Lion hunter days per treed lion	Lion hunter days per harvested lion
Coefficient of Variation	0.29	0.27	0.31	0.23
Duration of study (years) to detect an annual 25% change in population (β=0.5, α=0.05)	5	5	6	5
Probability (β) of detecting a 25% trend between years (α=0.05)	0.06	0.06	0.06	0.06

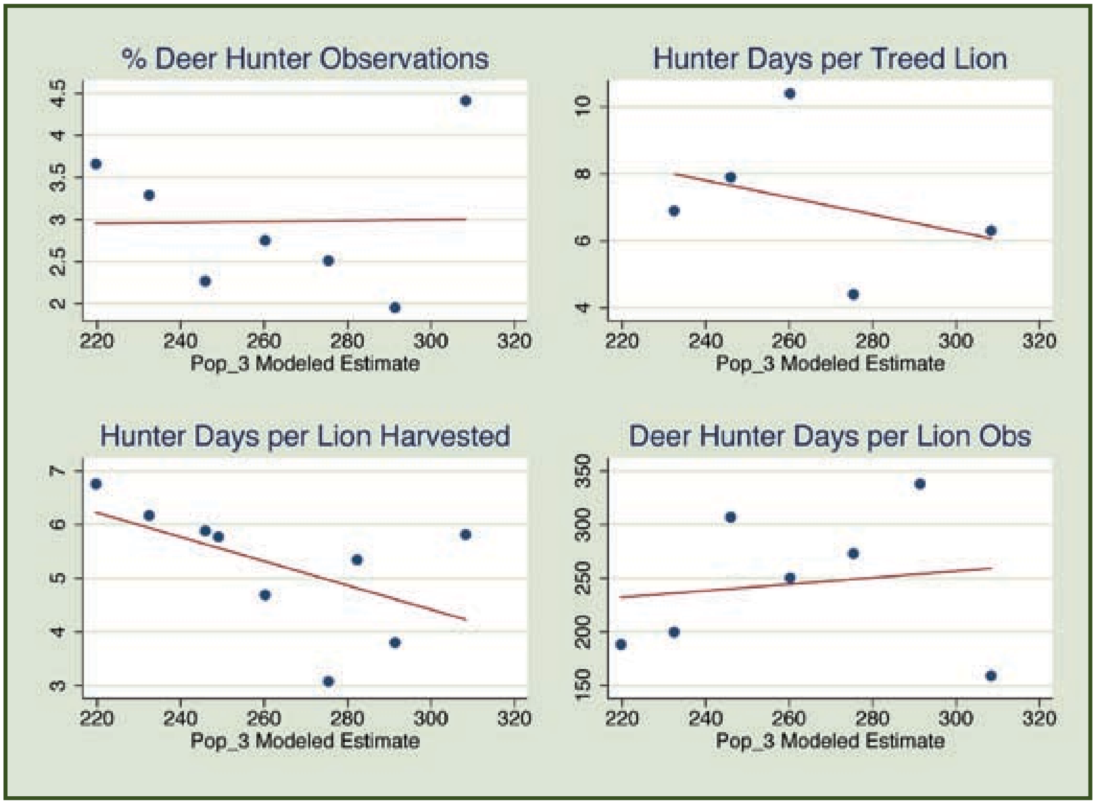


Figure 6.4. Relationship of hunter effort and modeled population estimate based on pop_3 model, 1998 to 2006 western Montana.

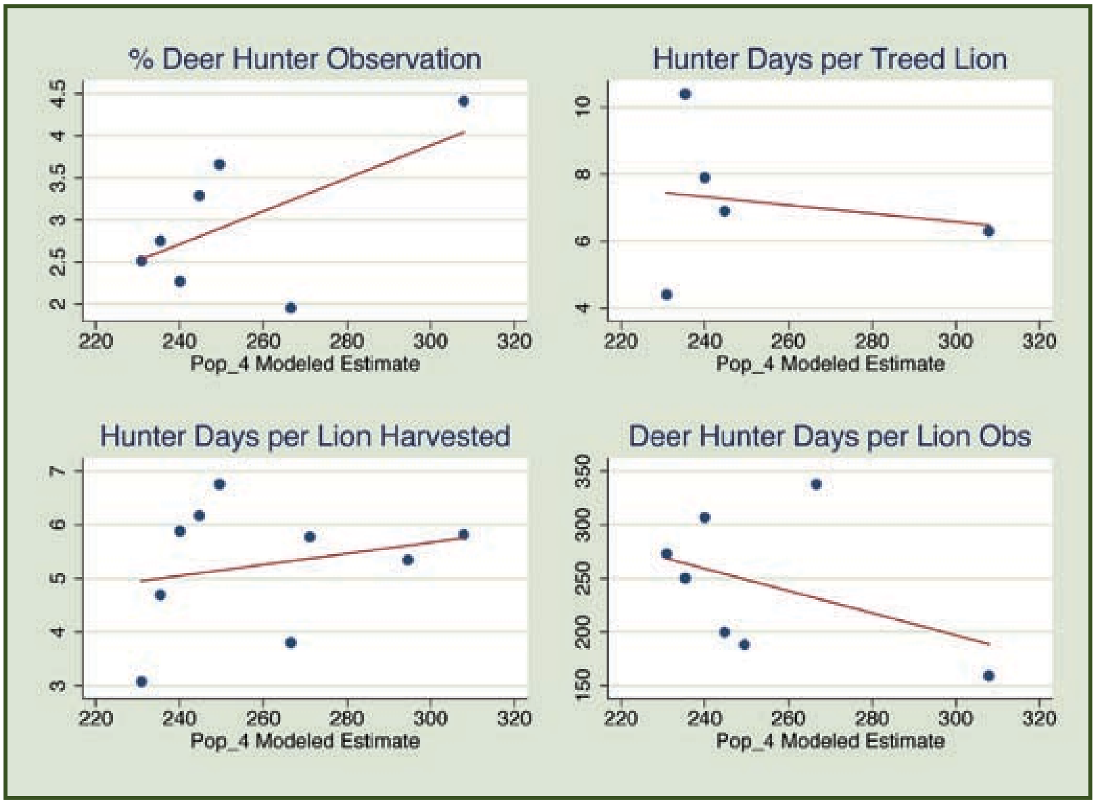


Figure 6.5. Relationship of hunter effort and modeled population estimate based on pop_4 model, 1998 to 2006 western.

in previous sections that population growth, and therefore any population model, is most dependent on female survival. We have also shown that quota levels affect survival. In each year of our study the female quota was filled or over achieved (Figure 6.2), reducing survival and therefore population growth. It may actually be the case that, with regard to female quotas, population growth rate or level is the dependent rather than independent variable. Similarly it is not unexpected then that we would find a significant relationship between our modeled population estimate and the proportion of the harvest that was female.

Biologist Tonya Chilton with Jed and houndsmen/biologist Brian Shinn at the Cap Wallace parking area on the Furbearer Mountain Lion Track Route in the northern portion of the Garnet Mountains. *(Photo courtesy of Jeff Sikich)*

We suggest that capture, based on intensive field efforts (i.e. searching for tracks in snow during winter) remains the best method of census for mountain lions.

Anderson and Lindzey (2005) suggested that adult females should be the least vulnerable to human harvest and that changes in age and percent of females in the harvest may be used as an index of population growth rate. Based on Barnhurst (1986) they argued that the probability of a mountain lion being harvested was a function of its relative abundance multiplied by its relative vulnerability (their propensity for crossing roads). It was assumed that resident females with young <6 months of age where least vulnerable and that their appearance in the harvest denoted a reduction in more vulnerable cohorts and thus a declining population. They suggested a harvest consisting of 25% females likely denoted a declining population while the population could sustain a harvest of 10-15% adult females. Our analysis showed both declining and increasing population growth rates above the 25% threshold (Figure 6.2) and Anderson and Lindzey's finding may simply demonstrate the perils associated with fixed quotas, namely quotas that do not match the existing population may lead to population decline, as much as an index of population level.

We suggest that capture, based on intensive field efforts (i.e. searching for tracks in snow during winter) remains the best method of census for mountain lions. However, this method is prohibitively expensive and time-consuming, which prevents its widespread use for lion conservation and management. A recent survey of state game agencies found that obtaining a method of quantifying mountain lion populations and trend was a research priority for most jurisdictions (Beausoleil et al. 2008). The need for easily-obtained and inexpensive indices is apparent, however our results add to a growing body of evidence that have found these techniques lacking (Beier and Cunningham 1996, Choate et al. 2006, Garshelis and Hristienko 2006). Many of the indices we evaluated were uncorrelated with our best independent measures of population sizes and trends, making their utilization detrimental to effective lion management programs and decisions. The measures that were correlated with our best independent measures of population size were imprecise, which in turn meant that their power to detect changes in lion population sizes, and therefore their utility for informing lion management is limited.

Summary, Management Implications and Recommendations - Section 7

Summary

Similar to past research, we found no effect of harvest on reproductive parameters (i.e. litter size, birth interval, maternity, age at dispersal, and first breeding). However, our research suggests that mountain lion populations are affected by human harvest, through its additive effects on survival of all age classes and a resultant disruption of juvenile dispersal. As such, wildlife managers through the use of human harvest, have the capability to limit mountain lion population growth.

We found that harvest was additive to other sources of mortality in kittens, independent juveniles and adults and contributed to low survival in all hunted age groups (i.e. kitten survival = 0.41, juvenile survival = 0.48, and adult survival = 0.59) effectively causing a cessation of emigration from the hunted Garnet study area prior to its protection. While maternity, the number of kittens born per female per year, was not significantly lower during hunting, survival of juveniles was low enough that during 3 years of study, with substantial harvest, only 2 of 12 collared juveniles survived to dispersal age. Harvest reduced the population in the Garnet by approximately 35% in three years, an annual growth rate of 0.88. Following the cessation of hunting the protected Garnet study area began producing emigrants to the surrounding Blackfoot drainage immediately. Beginning the first year after protection, between 60 and 100% of collared juveniles within the Garnet emigrated to an area outside the protected study area but still within the Blackfoot watershed.

Houndsmen/biologist Grover Hedrick with immobilized radio-collared adult female F11. (Photo courtesy of Melanie Trapkus)

The protection of the Garnet allowed it to act as a source population to the remainder of the Blackfoot drainage. This combined with reduced quotas and resultant increased survival outside the Garnet allowed the population

Wildlife managers through the use of human harvest, have the capability to limit mountain lion population growth.

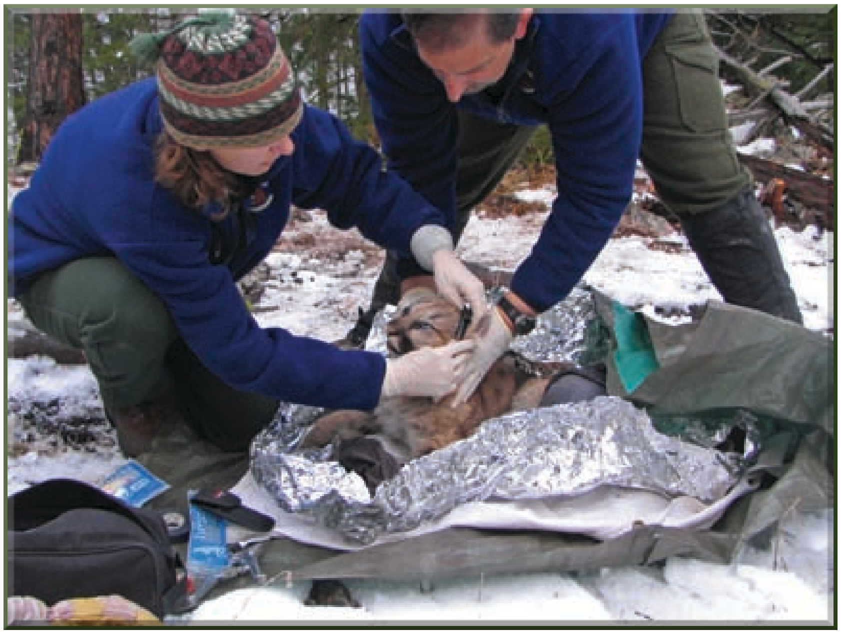
Houndsmen/biologist Brian Shinn with immobilized adult female F49. (Photo courtesy of Tonya Chilton)

Our results suggest that a protected area representing as little as 12% of the landscape in the Blackfoot watershed can act as a viable source.

to increase by approximately 6% a year, resulting in a total population by the end of 2006 close to initial population levels from 1997 when the study began. Our results suggest that a protected area representing as little as 12% of the landscape in the Blackfoot watershed (915km^2 of 7,908km^2) can act as a viable source. However, due to the additive nature of hunting to other mortality sources, only female quotas of 0 (or very low) are likely to increase survival of females to a level where dispersal is allowed to take place. We found that hunting shaped the survival structure of the population and that small incremental changes in quota levels did not reduce hunting mortality or increase population growth. Due to the high level of population growth sensitivity to adult female survival, mortality (harvest and natural combined) greater than 0.20 is likely to lead to population decline. This level of hunting pressure or greater may be desirable if population reduction is a management goal.

The population indices we evaluated were not well correlated with our best independent measure of population size, making their use for management decisions questionable. The best index we measured, when compared to our modeled population estimates, was of the percent of females in the harvest. However this could also be interpreted as another indication of the importance of female survival in population growth. Without some indication of the true population level it is hard to interpret how the percentage of females in the harvest would equate to a true mortality rate. Garshelis and Hristienko (2006), in comparing black bear harvest data, concluded that harvest indices are not precise or rigorous enough to provide useful information on population trend. In fact even the indices that best fit our modeled population estimates lacked enough precision to detect even a 25% annual change in population level over the span of less than 4 years.

Our results show the strong effect harvest can have on targeted populations through shaping survival, and even neighboring untargeted populations by affecting dispersal patterns. In order to set harvest



Biologists Vickie Edwards and Rich DeSimone radio-collaring 5 month old male kitten M106. (Photo courtesy of Melanie Trapkus) levels or quotas to achieve a precise lion population objective an accurate population estimate would be required; yet no such method appears readily available. We therefore recommend that Montana Fish Wildlife and Parks explore other methods of population estimation beyond the indices we tested here and/or harvest structure where less precise population estimates are required.

MANAGEMENT IMPLICATIONS

The management implications of our research findings are presented in bullet form below.

1. **Hunting is a very effective tool for managing mountain lion populations. Human harvest is an additive form of mortality that shapes the overall survival structure of mountain lion populations. Small reductions in quota levels appear ineffective at significantly altering survival.**
2. **Current indices of population level including track surveys, hunter effort and success, public observations, age of harvested lions, percent of quotas filled and percent of females in the harvest, lack the precision or correlation to population growth to provide useful indications of population level or trend.**
3. **We found that a protected area representing 12% of the landscape (915km^2) acted as a viable source population, increasing population growth of the surrounding hunted area by approximately 3% annually. This finding is in contrast to previous recommendations that 63% of mountain lion habitat may need to be protected in order to maintain viable lion populations (Laundre and Clark 2003). The protection of 12% of the landscape does not guarantee positive or stable growth rates. The size of reserve required to maintain a sink population is a function of source productivity and sink mortality.**
4. **Ultimately population growth is reliant on female survival. Adult female mortality > 20% (natural and harvest combined) is likely to cause a decrease in population level.**

Adult female F34 with GPS collar. (Photo courtesy of Grover Hedrick)

Ultimately population growth is reliant on female survival. Adult female mortality > 20% (natural and harvest combined) is likely to cause a decrease in population level.

Uncollared male lion treed in the Swan valley. (Photo courtesy of Scott Sciaretta)

MANAGEMENT RECOMMENDATIONS

We recommend lion population objectives and harvest quotas that account for this lack of precision.

Given the limitations of abundance estimation techniques currently available to wildlife managers, and the effect harvest can have on mountain lion populations, we recommend lion population objectives and harvest quotas that account for this lack of precision. A harvest system that will protect the biological integrity of mountain lion populations, while providing public harvest opportunity and flexibility to managers in addressing management concerns is desired. A source-sink management strategy, based on an experimental/adaptive management approach could be implemented as follows, depending on desired relative population densities in sink areas.

All management goals or treatments described below are dependent on the existence of a viable source population for males and protection of females. We found the Garnet, representing 12% of the total area, to be a viable source at the harvest levels observed in the surrounding Blackfoot watershed (i.e. juvenile and adult male survival rates of approximately 0.50). Male survival rates below these levels may require larger source areas to sustain reproduction in sink populations.

1. **Management goal of low relative abundance in sink area.**
    - General season for both independent males and females.
    - Areas managed at this level would theoretically consist of mainly juvenile immigrants from outside the focal area. Harvest therefore would likely consist of animals < 2-3 years of age. Little or no reproduction and zero dispersal would be expected.
2. **Management goal of moderate relative abundance in sink area.**
    - General season for independent males with some protection (i.e. low quotas or permit levels) for females.
    - Areas managed at this level would likely consist of low densities of mainly juvenile/immigrant males with only a few older age females. Moderate levels of productivity, with some female recruitment, with low levels of dispersal due to high juvenile male mortality would be expected.
3. **Management goal of high relative female abundance in sink area (female source).**
    - General season on independent males with full protection (i.e. 0 take) for females.
    - Areas managed at this level would likely consist of low

densities of mainly juvenile/ immigrant males, and older age females. Moderate levels of productivity and female dispersal, with low levels of male dispersal due to high juvenile male mortality would be expected.

4. **Management goal of moderate relative abundance of males and high relative abundance of females (partial source).**
   - Limited harvest of males (i.e. low quotas or permit levels) and full protection of females.
   - Areas managed at this level may consist of natural age distributions and moderate levels of dispersal due to increased juvenile survival.

5. **Management goal of focal source population (true source).**
   - Full protection of a contiguous area approximately 1000km^2 AND not less than 12% of the greater landscape, for not less than 5 years (i.e. 2 generations).
   - Areas managed at this level should consist of natural age and sex distributions, high reproduction and high dispersal.

In considering these concepts, our results show that a reserve as small as the Garnet study area may be able to act as a source to the surrounding watershed, thereby, in conjunction with protection of adult females, helping to create a stable or slowly growing population over the larger area. This finding has implications for harvest management in specific hunting districts or small areas. If the management goal in a particular area reflects stable or increasing relative lion abundance, a reserve juxtaposed within exploited areas should reduce the chance of overharvest and large swings in mountain lion populations that have been seen elsewhere, while maintaining or increasing harvest opportunity.

Conversely, if the management objective in a particular area is to reduce the relative density of lions, this finding implies that hunting regulations and the harvest structure in surrounding or nearby areas also needs to be considered; increased harvest pressure in a small area may not have lasting effects on relative lion abundance in that area as harvested animals are replaced through immigration.

A reserve juxtaposed within exploited areas should reduce the chance of overharvest and large swings in mountain lion populations that have been seen elsewhere

FUTURE RESEARCH

Current research undertaken by Montana Fish Wildlife and Parks may provide alternatives to the use of indices in mountain lion population estimation and potentially enable management of lion populations to achieve absolute population size objectives. DNA based mark-recapture uses established mark-

Biologists Melanie Trapkus and Doug Powell and MFWP veterinarian Mark Atkinson examining adult female F88. (Photo courtesy of Melanie Trapkus)

Resource selection of mountain lions estimated from these data and other studies may also have utility for informing the management of harvested populations, including mountain lions.

recapture statistical protocols and has shown some promise in estimating mountain lion abundance (Beausoleil et al. 2005). Russell et al. (in review) are currently exploring the use of DNA samples collected during this research project to estimate mountain lion abundance.

The results of this study may lend themselves to the use of Resource Selection Function (RSF) based population estimation. This study provides reference population estimates for the Garnet and Blackfoot watershed that can be applied to other areas of Montana based on resource selection of mountain lions estimated from these data and other studies. Linking animal abundance with resource selection functions (RSFs) is an extension of linear modeling and a recent focus in wildlife (Boyce and McDonald 1999, Pearce and Ferrier 2001). Boyce and McDonald's (1999) technique extrapolates animal density to a broader landscape by combining RSFs, and therefore the relative probability of occurrence, and density from a reference population. This technique has been used to test hypotheses regarding density of grizzly bears (*Ursus arctos*), and woodland caribou (*Rangifer tarandus caribou*) (Boyce and Waller 2003, Ciarniello et al. 2007, Seip et al. 2007). Other authors have built on Boyce and McDonald's method by combining RSF derived population densities with spatially explicit survival models to identify source and sink habitats in order to help guide recovery of threatened species (Aldridge and Boyce 2008, Nielsen et al. 2008). This technique may also have utility for informing the management of harvested populations, including mountain lions.

Radio-collared 5 week old kitten M21.
(Photo courtesy of Milo Burcham)

LITERATURE CITED - SECTION 8

Aalen, O. 1978. Nonparametric inference for a family of counting processes. Annals of Statistics 6:701-726.

Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. Israel Journal of Ecology and Evolution 54:389-419.

Anderson, C. R., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildlife Society Bulletin 33:179-188.

Anderson, P. K., O. Borgan, R. D. Gill, and N. Keiding. 1997. Statistical Models Based on Counting Processes. Springer, New York.

Arjo, W. M. 1998. The effects of recolonizing wolves on coyote populations, movements, behaviors, and food habits. University of Montana, Missoula, MT.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. N. D. O. Wildlife, editor. Reno, NV.

Aune, K. E. 1991. Increasing mountain lion populations and human-mountain lion interactions in Montana. Pages 114 *in* Proceedings of Mountain Lion-Human Interactions: Symposium and Workshop.

Balme, R. A., L. T. B. Hunter, P. Goodman, H. Ferguson, J. Craige, and R. Slotow. 2010. An adaptive management approach to trophy hunting og leopards (*Panthera pardus*): a case study from KwaZulu-Natal, South Africa. *in* D. Macdonald, and A. J. Loveridge, editors. The biology and conservation of wild felids. Oxford University Press, New York, NY.

Barnhurst, D. 1986. Vulnerability of cougars to hunting. Utah State University, Logan, UT.

Bart, J., S. Droege, P. Geissler, B. Peterjohn, and C. J. Ralph. 2004. Density estimation in wildlife surveys. Wildlife Society Bulletin 32:1242-1247.

Beausoleil, R. A., D. Dawn, D. A. Martorello, and C. Morgan. 2008. Cougar management protocols: a survey of wildlife agencies in North America. Pages 261 *in* Proceedings of Ninth Mountain Lion Workshop.261.

Beausoleil, R. A., K. I. Warheit, and D. A. Martorello. 2005. Using DNA to estimate cougar populations in Washington: a collarborative approach. Pages 238 *in* Proceedings of The 8th Mountain Lion Workshop.238.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94-108.

_____. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228-237.

Beier, P., and S. C. Cunningham. 1996. Power of track surveys to detect changes in cougar populations. Wildlife Society Bulletin 24:540-546.

Bellemain, E., A. Zedrosser, S. Manel, L. P. Waits, P. Taberlet, and J. E. Swenson. 2006. The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. Proceedings of the Royal Society B-Biological Sciences 273:283-291.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. TREE 14:268-272.

Boyce, M. S., and J. S. Waller. 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. Wildlife Society Bulletin 31:670-683.

Boyko, R. H., and A. J. Marshall. 2009. The willing cuckold: optimal paternity allocation, infanticide and male reproductive strategies in mammals. Animal Behavior 77:1397-1407.

Brainerd, S. M. 1985. Reproductive ecology of bobcats and lynx in western Montana. Thesis, University of Montana, Missoula, MT.

Buckland, S. T. 2001. Introduction to distance sampling : estimating abundance of biological populations. Oxford University Press, Oxford ; New York.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic Approach. Springer-Verlag, New York.

_____. 2002. Model selection and multimodel inference : a practical information-theoretic approach. 2nd edition. Springer, New York.

Caley, P. A., and C. G. Morley. 2002. Assessing growth rates of European rabbit populations using spotlight transect counts. Journal of Wildlife Management 66:131-137.

Caswell, H. 2001. Matrix population models : construction, analysis, and interpretation. Sinauer Associates, Sunderland, Mass.

Chepko-Sade, B. D., Z. T. Halpin, and American Society of Zoologists. 1987. Mammalian dispersal patterns : the effects of social structure on population genetics. University of Chicago Press, Chicago.

Choate, D. M. 2009. Cougar-induced behavioral plasticity: ungulate behavior under the risk of predation on the National Bison Range. Dissertation, University of Notre Dame, Notre Dame, IN.

Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782-799.

Ciarniello, L. M., N. S. Boyce, D. C. Heard, and D. R. Seip. 2007. Components of grizzly bear habitat selection: Density, habitats, roads, and mortality risk. Journal of Wildlife Management 71:1446-1457.

Cleves, M. A., W. W. Gould, and R. G. Gutierrez. 2004. An introduction to survival analysis using Stata. Stata Press, College Station, Tex.

Cooley, H. S., H. S. Robinson, R. B. Wielgus, and C. S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. Journal of Wildlife Management 72:99-106.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913-2921.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. WildFutures, Bainbridge Island, Wash.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187-&.

D'eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430-439.

Eberhardt, L. L., and M. A. Simmons. 1987. Calibrating population indices by double sampling. Journal of Wildlife Management 51:665-675.

Errington, P. L. 1956. Factors Limiting Higher Vertebrate Populations. Science 124:304-307.

Fernandez-Gil, A., J. E. Swenson, C. Granda, T. Perez, A. Dominguez, A. Ordiz, J. Naves, and M. Delibes. 2010. Evidence of sexually selected infanticide in an endangered brown bear population. Animal Behaviour 79:521-527.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58-63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Garshelis, D. L., and H. Hristienko. 2006. State and provincial estimates of American black bear numbers versus assessments of population trend. Ursus 17:1-7.

Gerrodette, T. 1993. Trends - Software for a Power Analysis of Linear-Regression. Wildlife Society Bulletin 21:515-516.

Getz, W. M., and R. G. Haight. 1989. Population harvesting : demographic models of fish, forest, and animal resources. Princeton University Press, Princeton, N.J.

Grambsch, P. M., and T. M. Therneau. 1994. Proportional Hazards Tests and Diagnostics Based on Weighted Residuals. Biometrika 81:515-526.

Greenwood, P. J. 1980. Mating Systems, Philopatry and Dispersal in Birds and Mammals. Animal Behaviour 28:1140-1162.

Gude, J. A., C. Hinz, J. Dykstra, B. Beardslee, and K. E. Aune. 2006. Deer hunting and harvest report, license year 2005. Montana Department of Fish, and Parks, Helena, MT. 620 pp.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668-674.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544-1555.

Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275-1284.

Horne, J. S., and E. O. Garton. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641-648.

Hornocker, M. G. 1969. Winter Territoriality in Mountain Lions. Journal of Wildlife Management 33:457- 464.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. Wiley, New York.

Hosmer, D. W., S. Lemeshow, and S. May. 2008. Applied survival analysis : regression modeling of time-to-event data. 2nd edition. Wiley-Interscience, Hoboken, N.J.

Inskip, C., and A. Zimmermann. 2009. Review Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43:18-34.

Jackson, P., and K. Nowell. 1996. Problems and possible solutions in management of felid predators. Journal of Wildlife Research 1:304-314.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the Andersen-Gill model to Yellowstone grizzly bears. Journal of Wildlife Management 68:966-978.

Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753-1765.

Johnson, M. L., and L. K. Couch. 1954. Determination of the abundance of cougar. Journal of Mammalogy 35:255-256.

Kalbfleisch, J. D., and R. L. Prentice. 1980. The statistical analysis of failure time data. Wiley, New York.

Kaplan, E. L., and P. Meier. 1958. Nonparametric-Estimation from Incomplete Observations. Journal of the American Statistical Association 53:457-481.

Keister, G. P., and W. A. Van Dyke. 2002. A predictive population model for cougars in Oregon. Northwest Science 76:15-25.

Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. Journal of Mammalogy 89:408-418.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages xvii, 474 p. *in* Radio Tracking and Animal Populations. Academic Press,San Diego.

Knopff, K. H. 2010. Cougar Predation in a Multi-Prey System in West-Central Alberta. Dissertation, University of Alberta, Edmonton, AB.

Knopff, K. H., A. A. Knopff, and M. S. Boyce. 2010. Scavenging Makes Cougars Susceptible to Snaring at Wolf Bait Stations. Journal of Wildlife Management 74:644-653.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: An interface between biology and management. Journal of Range Management 52:398-412.

Kunkel, K. 1997. Predation by wolves and other large carnivores in northwestern Montana and southeastern British Columbia. University of Montana, Missoula, MT.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246-254.

Larue, M. A., and C. K. Nielsen. 2008. Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecological Modelling 212:372-381.

Laundre, J., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159-170.

Lehmkuhl, J. F. 1981. Distribution and habitat selection of elk in the northern Garnet Mountains of western Montana. . M.S. Thesis, University of Montana, Missoula, MT.

Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. Journal of Wildlife Management 58:1994.

Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. Wildlife Society Bulletin 20:224-227.

Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation 4:345-349.

Logan, K. A., L. L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648-654.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma : evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC.

Lohr, S. 2009. Sampling : design and analysis. 2nd Ed. edition. Cengage Brooks/Cole, Boston, MA.

Maehr, D. S., and G. B. Caddick. 1995. Demographics and Genetic Introgression in the Florida Panther. Conservation Biology 9:1295-1298.

Maletzke, B. T. 2010. Effects of anthropogenic disturbance on landscape ecology of cougars. Washington State University, Pullman, WA.

Marchandeau, S., J. Aubineau, F. Berger, J. C. Gaudin, A. Roobrouck, E. Corda, and F. Reitz. 2006. Abundance indices: reliability testing is crucial - a field case of wild rabbit Orydolagus cuniculus. Wildlife Biology 12:19-27.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

Mills, L. S. 2007. Conservation of wildlife populations : demography, genetics, and management. Blackwell Pub., Malden, MA.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology : theory and practice of population viability analysis. Sinauer Associates, Sunderland, Mass.

Moscovice, L. R., A. Di Fiore, C. Crockford, D. M. Kitchen, R. Wittig, R. M. Seyfarth, and D. L. Cheney. 2010. Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. Animal Behaviour 79:1007-1015.

Murphy, K. 1983. Relationships between a mountain lion population and hunting pressure in western Montana. University of Montana.

_____. 1998. The ecology of the cougar (Puma concolor) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans, University of Idaho, Moscow, ID.

Murray, D. L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530-1543.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514-2524.

Nelson, W. 1972. Theory and applications of hazard plotting for censored failure data. Technometrics 14:945-965.

Nielsen, S. E., G. B. Stenhouse, H. L. Beyer, F. Huettmann, and M. S. Boyce. 2008. Can natural disturbance-based forestry rescue a declining population of grizzly bears? Biological Conservation 141:2193-2207.

Oregon Department of Fish and Wildlife. 2006. 2006 Oregon Cougar Management Plan. Pages 135 Salem, OR,

Packer, C., M. Kosmala, H. S. Cooley, H. Brink, L. Pintea, D. Garshelis, G. Purchase, M. Strauss, A. Swanson, G. Balme, L. Hunter, and K. Nowell. 2009. Sport Hunting, Predator Control and Conservation of Large Carnivores. Plos One 4:-.

Pearce, J., and S. Ferrier. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. Biological Conservation 98:33-43.

Pepe, M. S., and M. Mori. 1993. Kaplan-Meier, Marginal or Conditional-Probability Curves in Summarizing Competing Risks Failure Time Data. Statistics in Medicine 12:737-751.

Peto, R., and J. Peto. 1972. Asymptotically efficient rank invariant test procedures. Journal of the Royal Statistical Society Series a-General 135:185-206.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences of the United States of America 95:213-218.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size. Ecology 81:1533-1543.

Pintilie, M. 2006. Competing risks : a practical perspective. John Wiley & Sons, Chichester, England ; Hoboken, NJ.

Prentice, R. L. 1978. Linear rank-tests with right censored data. Biometrika 65:167-179.

Quigley, H., and M. G. Hornocker. 2010. Cougar population dynamics. *in* M. G. Hornocker, andS. Negri, editors. Cougar : ecology and conservation, The University of Chicago Press, Chicago; IL.

Raithel, J. D. 2005. Impact of calf survival on elk population dynamics in west-central Montana. M. S. Thesis, University of Montana, Missoula, MT.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.

Ray, J. C., K. H. Redford, R. S. Steneck, and J. Berger. 2005. Large carnivores and the conservation of biodiversity. Island Press, Washington.

Riley, S. J. 1998. Integration of environmental, biological, and human dimensions for managment of mountain lions (*Puma concolor*) in Montana. Cornell University, Ithaca, NY.

Riley, S. J., and D. J. Decker. 2000. Wildlife stakeholder acceptance capacity for cougars in Montana. Wildlife Society Bulletin 28:931-939.

Riley, S. J., and R. A. Malecki. 2001. A landscape analysis of cougar distribution and abundance in Montana, USA. Environmental Management 28:317-323.

Riley, S. P. D., C. Bromley, R. H. Poppenga, F. A. Uzal, L. Whited, and R. M. Sauvajot. 2007. Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. Journal of Wildlife Management 71:1874-1884.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: Cougar demography and immigration in a hunted population. Ecological Applications 18:1028-1037.

Rogers, A. R., A. P. Carr, L. Smith, and J. G. Kie. 2005. HRT: Home Range Tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Ecosystem Research.

Root, K. V. 2004. Florida panther: using models to guide recovery efforts. Pages 491-504 in H. R. Akcakaya, M. A. Burgman, O. Kindvall, C. C. Wood, P. Sjogren-Gulve, andJ. S. Hatfield, editors. Species conservation and management : case studies. Oxford Univ. Press,New York, NY.

Ross, I. P., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Canadian Journal of Zoology 74:771-775.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. Journal of Wildlife Management 56:417-426.

Russell, R. E., J. A. Royle, R. DeSimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim, and K. S. McKelvey. In review. Estimating abundance from unstructured spatial samples: an example with Montana mountain lions (Puma concolor).

Ruth, T. K. 2004. Patterns of resource use among cougars and wolves in northwestern Montana and southeastern British Columbia. University of Idaho, Moscow, ID.

Ruth, T. K., and P. C. Buotte. 2007. Cougar ecology and cougar-carnivore interactions in Yellowstone National Park. Final technical report. H. W. I. W. C. Society, editor. Bozeman, MT.,

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:3 - 60.

Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71:1539-1544.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London ; New York.

Sinclair, A. R. E., J. M. Fryxell, and G. Caughley. 2006. Wildlife ecology, conservation, and management. 2nd edition. Blackwell Pub., Malden, MA ; Oxford.

Solomon, M. E. 1949. The natural control of animal populations. Journal of Animal Ecology 18:1-35.

Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. Journal of Wildlife Management 60:962-969.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: Implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588-1600.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798-808.

Swihart, R. K., and N. A. Slade. 1985. Influence of Sampling Interval on Estimates of Home-Range Size. Journal of Wildlife Management 49:1019-1025.

Taylor, S. K., C. D. Buergelt, M. E. Roelke-Parker, B. L. Homer, and D. S. Rotstein. 2002. Causes of mortality of free-ranging Florida panthers. Journal of Wildlife Diseases 38:107-114.

Thompson, S. K. 2002. Sampling. 2nd edition. Wiley, New York.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350-1356.

Treves, A., R. B. Wallace, and S. White. 2009. Participatory Planning of Interventions to Mitigate Human-Wildlife Conflicts. Conservation Biology 23:1577-1587.

Van Dyke, F. G., R. H. Brocke, and H. Shaw. 1986. Use of road track counts as indices of mountain lion presence. Journal of Wildlife Management 50:102-109.

Van Sickle, W., and F. G. Lindzey. 1991. Evaluation of a cougar population estimator based on probability sampling. Journal of Wildlife Management 55:738-743.

Van Sickle, W. D., and F. G. Lindzey. 1992. Evaluation of road track surveys for cougars (Felis concolor). Great Basin Naturalist 52:232-236.

White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288-331 in L. Boitani, andT. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press,New York.

Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. Nature 428:175-178.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations : modeling, estimation, and decision making. Academic Press, San Diego.

Williams, J. 1992. Ecology of mountain lions in the Sun River area of Northern Montana. Montana State University, Bozeman, MT.

Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages 351-380 *in* J. J. Millspaugh, andJ. M. Marzluff, editors. Radio tracking and animal populations. Academic Press,San Diego.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. Ecology 81:628-641.

Worton, B. J. 1995. Using Monte-Carlo Simulation to Evaluate Kernel-Based Home-Range Estimators. Journal of Wildlife Management 59:794-800.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, N.J.

Zimmermann, F., C. Breitenmoser-Wursten, and U. Breitenmoser. 2005. Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. Journal of Zoology 267:381-395.

Radio-collared subadult female F55. (Photo courtesy of Brian Shinn)

Lion Painting (Courtesy of Robert Neaves)