Population Demographics of Cougars in the Black Hills:
Survival, Dispersal, Morphometry, Genetic Structure,
and Associated Interactions with Density Dependence

by

Daniel J. Thompson

A dissertation submitted in partial fulfillment of the requirements for the
Doctor of Philosophy
Major in Wildlife and Fisheries Sciences
South Dakota State University
2009
Population Demographics of Cougars in the Black Hills: Survival, Dispersal, Morphometry, Genetic Structure, and Associated Interactions with Density Dependence

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Jonathan A. Jenks 17 Nov 2009
Dissertation Advisor

Dr. David W. Willis 11/7/09
Date
Head, Department of Wildlife and Fisheries Sciences
ACKNOWLEDGEMENTS

Any fairly intense field project has so many thanks that there are bound to be some folks left out and for that I want to apologize right now. First I’d like to thank Jack Alexander for taking a used to be “flatlander” and teaching me the ways of the mountain lion. Jack knows more about lions than anyone in South Dakota and he tried to share some of that knowledge with me along with becoming a true friend. I need to thank the many folks from South Dakota Game Fish and Parks who assisted with captures: John Kanta, Steve Griffin, Lowell Schmitz, Gene Galinat, Lane Severs, Tim Bradeen, Mike Kintigh, Ted Benzon, Blaire Waite, Smilin’ Chad, Rick Halseth, and many others who assisted from the shadows. I’d like to thank Les Flack who went above and beyond the call of any wildlife volunteer and is a very big reason that cougar research continues today in the Black Hills. I hope we can go on a few more chases Les! I need to thank Muck Morrison for volunteering many hours of field work while tracking radioed cougars. Thanks for the laughs and good times Muck! Also thanks to Jeff Olson, Todd Brinkman, and all the private landowners who allowed access to their lands throughout the course of the project. The ranchers, landowners and homeowners of the Black Hills were very cooperative and helpful when it came to aspects of working with lions in sometimes tricky situations.

Maybe most importantly I need to thank Dale, Dave, Freckles, Moe, Pancho, Pepper, Tank, Tracker and even little ol’ Wilson for helping us out so much with capture and letting us hear the melodic sound of a hound on tree.
I want to personally thank my advisor Dr. Jon Jenks for taking a chance on a punk like myself and throwing me literally into the lion’s den. I’ve learned a great deal from you and also gained a friend along the way. The many conversations about the in’s and out’s of the wildlife biology field will always be remembered. Also thanks to my committee members, Chip Leslie, Dan Hubbard, Zeno Wicks and Thomas Stenvig for help, mentoring, and some mighty fun discussions. Zeno thanks for giving me the opportunities to run to through the wilds of Africa! Extreme thanks to Terri, Di, and Carol at SDSU—without them the department would be in shambles.

Rather than leave anyone out I’d like to thank all the graduate students at SDSU for helping along the way. I do need to thank Teresa Zimmerman, Emily Lorenzen, Dustin Shaible, Krysten Schuler, Jamie Wheeler, and Sheila Thomson for assisting with necropsies. (Somehow you got me to appreciate the foul mess Dr. Zimmerman.) This is one of the stinkiest jobs in the world, and your assistance and laughter greatly helped along the process.

I need to thank all the pilots from the Civil Air Patrol for providing telemetry flights on radiocollared animals. Especially Leo Beeht and Gerald Kirk who took the bulk share of flights. You guys were great to work with and I appreciate your flexibility and the fact that I never puked…despite your best efforts Leo! This study was funded by Federal Aid to Wildlife Restoration Fund Project W-75-R (Study No. 7594) administered by the South Dakota Department of Game, Fish, and Parks (SDGFP), in addition to funds received from Safari Club International.
Thanks to my “cougar colleagues”, especially Chuck Anderson, Fred Lindzey, Dorothy Fecske, Kerry Murphy, and Toni Ruth. All of you were there to help answer questions when they came up, and they often did. I look forward to continue collaborating with you on projects in the future. Brian (Jansen) thanks for keeping track of those subadults! Thank you to all my cronies in the Wyoming Game and Fish Department for helping me through the neuroses of a full time job and finishing the game…

I would’ve never been in this position if not for the support of my many friends and family. I met and maintained a lot of outstanding friends during the course of this adventure. Thanks for sticking with me despite my frequent absence at holidays and family events so I could stay in the field Mom and Dad. I know better than to start naming specific friends that helped along the way from California to Terril, Iowa and Alaska to Burkina Faso and back--thanks all of you for keeping me in line, for the most part. And Mr Mojo Risin, I never took you on an actual lion chase but you definitely helped me keep some amount of sanity while working on this project over the last several years; which I might add were some of the best years of my life! Thanks to everyone involved and anyone I missed!!!!!
DEDICATION

I have a double dedication: I must dedicate this work to the memory of Mr Mojo Risin, (the hound not the rock poet) who didn’t make it to help me grasp that damn light at the end, but without her help I would’ve never made it past the flickering glow; and to my brother Mike (Big Mike) Thompson who always made me appreciate the ability to work on a project like this and for the opportunities I was lucky enough to receive and appreciate more because of you.
Abstract

Population Demographics of Cougars in the Black Hills:
Survival, Dispersal, Morphometry, Genetic Structure,
and Associated Interactions with Density Dependence

Daniel J. Thompson

2009

The cougar (*Puma concolor*) is the remnant apex predator of South Dakota. Cougars were extirpated from the majority of the Dakotas by the early 1900s, and severely reduced or extirpated from the Black Hills of South Dakota and Wyoming during this same time. Many factors led to the demise of cougars throughout North America, but cougars proved resilient. A few sporadic sightings were recorded in the Black Hills during the 20th century, with enough verified sightings occurring during the 1980s that the South Dakota Department of Game, Fish and Parks began recording sightings and verifying potential cougars. Verified reports continued and research was initiated in 1998 to document distribution and abundance of the species in the Black Hills. Early research efforts spawned the research that is included in this dissertation. The cougar population of the Black Hills rebounded to that of a viable breeding cougar population and is unique in that it naturally reestablished and also is semi-isolated from extant cougar populations. Our research encompassed the Black Hills of South Dakota and Wyoming (approximately 8,400 km²). Primary objectives were to: 1) document cougar survival by
sex and age class and characterize mortality of an unhunted cougar population, 2) document dispersal movements and assess philopatry of a cougar population semi-isolated from other populations in a mountainous region surrounded by atypical cougar habitat, 3) assess the genetic structure of a semi-isolated cougar population, 4) document morphological attributes of a newly recolonized cougar population, and 5) assess population status and document effects of density dependence as they relate to overall population demographics of the cougar population in the Black Hills. Cougars were captured and fitted with radio-transmitters to assess these objectives as well as acquiring ancillary data through sightings, reported mortalities, and cooperative efforts from many management agencies across several jurisdictional boundaries. Annual survival of independent adult cougars averaged 0.87 (range: 0.50 - 1.0 annually); no difference in survival ($P = 0.83$) occurred between adult males and females. Subadult males had the lowest survival rate (0.62) of any sex/age class in our study area. Kitten survival was 0.67. We documented 85 mortality events in South Dakota from 1998 - 2005. Vehicles (32.9%) and depredation removals (21.2%) accounted for most cougar mortality in the Black Hills, with 85% of mortality being human-induced. Males dispersed (Mean = 274.7 km SE 88.3) farther than females (Mean = 48.0 km SE 10.9), with females exhibiting 40% philopatry. No subadult males were recruited into the Black Hills cougar population. We documented several ($n = 6$) long-distance dispersal movements (>200 km) of male cougars and hypothesize that males making long-distance movements were in search of available mates. Movements documented by our study indicate that cougar range expansion and habitat recolonization are occurring. Cougars in the Black Hills
were comparable in size and weight to cougar populations in western North America. Regression analyses indicated that plantar pad width from front and hind feet were accurate indicators of sex of cougars > 1 year of age. Accurate measurements from reliable tracks may be useful for biologists to assess gender; however, age does not correlate as well with track dimensions. Although cougars in the Black Hills showed a marginally significant genetic bottleneck, they do not appear to have deleterious effects from the event. Cougars in South Dakota had an average expected heterozygositiy ($H_E$) of 0.542 and observed heterozygosity ($H_O$) of 0.547. Effective population size ($N_e$) of Black Hills cougars was 28 individuals (23 - 39; 95% CL). Based on our results, there is adequate power to discern individual cougars from geographically close (< 200 km) populations using 20 loci, and we recommend that a large-scale genetic database of cougars at an international level be constructed to assess genetic structure and population demographic across the species’ distribution. We identified several primary factors indicating density dependent effects on cougars in the Black Hills: decrease in female home-range size, increased home-range overlap, increased female dispersal and decreased philopatry, neonate sex ratios skewed to male, increased mortality related to intraspecific strife, infanticide and emaciation, and a decrease in body condition. Results will be used to assess initiation of harvest on the cougar population in the Black Hills as well as serving as fundamental baseline data to evaluate the status of the population in the future and assessment of management strategies to maintain the population in perpetuity.
TABLE OF CONTENTS

Acknowledgements...........................................................................................................iii
Dedication..........................................................................................................................vi
Abstract............................................................................................................................vii
LIST OF TABLES BY CHAPTER.................................................................xiii
LIST OF FIGURES BY CHAPTER.................................................................xv
APPENDIX A: CAPTURE MEASUREMENTS..................................................122

CHAPTER 1. GENERAL INTRODUCTION

General Introduction........................................................................................................1
Literature Cited..................................................................................................................5

CHAPTER 2. SURVIVAL AND MORTALITY CHARACTERISTICS OF AN
UNHUNTED COUGAR POPULATION IN THE BLACK HILLS OF SOUTH
DAKOTA

Abstract.........................................................................................................................9
Introduction....................................................................................................................10
Study Area....................................................................................................................12
Methods.......................................................................................................................13
Results...........................................................................................................................15
Discussion......................................................................................................................17
Management Implications...............................................................................................21
Literature Cited..............................................................................................................23
CHAPTER 3. DISPERSAL MOVEMENTS OF SUBADULT COUGARS FROM THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING: THE NOTIONS OF RANGE EDGE, RANGE EXPANSION, AND RECOLONIZATION

Abstract ........................................................................................................33
Introduction ..................................................................................................34
Study Area ....................................................................................................36
Methods ........................................................................................................37
Results ...........................................................................................................38
Discussion .....................................................................................................39
Management Implications .............................................................................43
Literature Cited ............................................................................................45

CHAPTER 4. MORPHOLOGICAL CHARACTERISTICS OF COUGARS IN THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING: PREDICTING COUGAR AGE AND SEX FROM OBTAINABLE FIELD DATA

Abstract ........................................................................................................53
Introduction ..................................................................................................54
Study Area ....................................................................................................55
Methods ........................................................................................................57
Results ...........................................................................................................58
Discussion .....................................................................................................59
Management Implications .............................................................................61
Literature Cited ............................................................................................62
CHAPTER 5. GENETIC STRUCTURE OF A GEOGRAPHICALLY DISJUNCT
RECOLONIZED COUGAR POPULATION: THE BLACK HILLS COUGAR

Abstract .............................................................................................................71
Introduction .......................................................................................................72
Study Area .........................................................................................................74
Methods ...........................................................................................................75
Results ...............................................................................................................77
Discussion .........................................................................................................78
Management Implications ..................................................................................80
Literature Cited ..................................................................................................81

CHAPTER 6. INDICATORS OF DENSITY DEPENDENCE IN A SEMI-
ISOLATED RECOLONIZED COUGAR POPULATION

Abstract .............................................................................................................91
Introduction .......................................................................................................92
Study Area .........................................................................................................95
Methods ...........................................................................................................96
Results ...............................................................................................................99
Discussion .........................................................................................................101
Management Implications ................................................................................104
Literature Cited ................................................................................................106

AUTHORS NOTE: The verbiage for the text (We versus I) was selected to articulate the point that research endeavors are rarely a singular effort from data collection to synthesis of the data to printed form.
LIST OF TABLES BY CHAPTER

CHAPTER 2.

Table 2.1 - Annual survival estimates for independent aged cougars in the Black Hills of South Dakota, 1999 – 2005 ......................................................29

CHAPTER 4.

Table 4.1 - Morphological characteristics (Mean ± 1 SE) of cougars from the Black Hills of South Dakota and Wyoming, 1998 - 2007 .............................66

Table 4.2 - Correlation data for male cougars (>1 yr of age) in the Black Hills of South Dakota and Wyoming .................................................................67

Table 4.3 - Correlation data for female cougars (>1 yr of age) in the Black Hills of South Dakota and Wyoming .................................................................67

CHAPTER 5.

Table 5.1 - Genetic variability by locus of samples taken from South Dakota and North Dakota cougars .................................................................87

Table 5.2 - Mean and Standard Error of genetic variability metrics for Dakota cougars ........................................................................................................88

Table 5.3 - Population assignment tests between North Dakota and South Dakota cougars using 20 microsatellite loci .......................................................89

Table 5.4 - Comparison of observed heterozygosity (H₀) levels of cougars in the Black Hills with other cougar populations and other carnivore species .......90
CHAPTER 6.

**Table 6.1**-Annual survival rate estimates \((S_i)\) for independent aged cougars in the Black Hills of South Dakota and Wyoming, 1999 – 2005

**Table 6.2**-Annual home-range (HR) values (Mean \(\pm\) 1 SE) for adult cougars in the Black Hills of South Dakota and Wyoming, 1999 – 2005
LIST OF FIGURES OF CHAPTER

CHAPTER 1.

**Figure 1.1**-Map of Black Hills study area located in western South Dakota and eastern Wyoming, encompassing approximately 8,400km²...........................8

CHAPTER 2.

**Figure 2.1**-Breakdown (%) of mortality events \( n = 85 \) documented for cougars in South Dakota, 1998 – 2005.................................................................30

**Figure 2.2**-Yearly breakdown of annual cougar mortality events documented in South Dakota, 1998 – 2005.................................................................31

**Figure 2.3**-Comparison between male and female cougar mortalities in the Black Hills of South Dakota, 1998 - 2005; (categories represent primary sources of mortality).................................................................32

CHAPTER 3.

**Figure 3.1**-Long-distance dispersal movements by subadult male cougars from the Black Hills of South Dakota, 2003 - 2006.................................51

**Figure 3.2**-Dispersal movements by subadult female cougars from the Black Hills of South Dakota, 2003 - 2007.................................52

CHAPTER 4.

**Figure 4.1**-Diagram of plantar pad measurements (mm) for front and hind feet of cougars sampled from the Black Hills of South Dakota and Wyoming..........................68
Figure 4.2-Template to determine sex of unknown cougar track impressions using plantar pad measurements of front and hind foot impressions………..69

CHAPTER 6.

Figure 6.1-Breakdown (%) of mortality events \( (n = 85) \) documented for cougars in South Dakota, 1998 – 2005…………………………………………………………117

Figure 6.2-Annual cougar mortality events documented in South Dakota, 1998 – 2005…………………………………………………………………118

Figure 6.3-Annual mortality events attributed to removal of nuisance animals (depredation and human safety risk), and
emaciation/starvation in the Black Hills, 2000 – 2006…………………………119

Figure 6.4-Annual number of reported cougar sightings in South Dakota, 1996 -2006………………………………………………………………120

Figure 6.5-Examples of facial scarring of adult male cougars due to intraspecific encounters in the Black Hills, 2004 – 2006 …………………… 121
CHAPTER 1: GENERAL INTRODUCTION

Few wild animals in the North American culture represent wildness, embody strength, stir emotion, and invoke fear as does the cougar (*Puma concolor*). The cougar goes by a multitude of common names (i.e., mountain lion, puma, panther, catamount, painter, cucuaguaranana) depending on personal and regional preferences, yet all referring to the same species of animal. (For purposes of the dissertation we chose to refer to *Puma concolor* as cougar throughout the text.) Roosevelt (1926) said of the cougar “It is itself a more skillful hunter than any human rival…it is a beast of stealth and rapine; its great velvet paws never make a sound, and it is always on watch whether for prey or for enemies”. The cougars’ presence in the western hemisphere has been known and documented by European settlers for more than 500 years, beginning with Columbus who first noted their existence in Honduras and Nicaragua (Young and Goldman 1946), and the species has long been an iconic figure in Native American culture (Young and Goldman 1946, Logan and Sweanor 2001). The sheer adaptability of cougars is represented by their distribution being the largest of any terrestrial mammal other than humans in the western hemisphere, ranging from the southern tip of Chile to the Yukon Territory (Logan and Sweanor 2000).

Cougars were first described in South Dakota by some of the early western exploratory expeditions. Lewis and Clark (2002) wrote of seeing large catlike animals along the Missouri River in the Dakotas. Exploratory expeditions to the Black Hills during the latter portions of the 19th century commented on seeing cougars while in the region; Ludlow believed the cougar to be “numerous” in the Black Hills (Ludlow 1875,
Turner 1974). Roosevelt (1926) stated that “though the cougar prefers woodland, it is not necessarily a beast of dense forests only; for it is found in all plains country, living in the scanty timber belts which fringe the streams, or among the patches of brush in the Badlands,” referring to cougars in other regions of the Dakotas.

The Black Hills ecosystem itself congers up images of a mysterious place that eerily rises from the prairie and makes its presence known. Lieutenant Colonel Dodge wrote of the Black Hills during the Newton-Jenney expedition of 1875 (Kime 1996): “Far out of the ordinary lines of plains travel…the Black Hills loomed up in silent majesty, mysterious, unknown…The Indians, maintained, when questioned about it, the most studied silence, or, even in their most confidential or drunken moments, gave such evasive and unsatisfactory replies as added tenfold to the strength of the mysterious fascination which existed in regard to it…The Black Hills has been to the plains traveler the embodiment of the fullest idea of the mysterious and the unknown.” Supplement the aura of Black Hills mysticism with one of the most heralded and cryptic creatures of the American West, and an extraordinary story begins to unfold.

Although thought to be plentiful at one time, bounty and unregulated hunting of cougars, along with market hunting of their prey, resulted in extirpation of the species from most if not all of South Dakota (Higgins et al. 1994). Although no records maintain certainty as to their complete demise, it was thought that cougars were nearly, if not completely, extirpated from the Black Hills around the turn of the 20th Century (Froiland 1990, Higgins et al. 2000). Sporadic sightings of cougars in the Black Hills occurred throughout the 1900s. In 1973, the Endangered Species Act was enacted in the United
States to protect animals at risk of future extinction. In South Dakota, the cougar was classified as a state threatened species in 1978, which gave the animals protection from unregulated take (Fecske 2003).

The 20th Century was an amazing time of change for the overall Black Hills ecosystem that in many ways was beneficial to the cougar population. In the latter part of the 1800s forested regions of the Black Hills were composed of all age classes of trees and the forest appeared irregular and broken (Graves 1899), primarily due to natural fires that created a mosaic within the forest system (Parrish et al. 1996). After 1900, fire suppression was initiated in the Black Hills, which changed the overall system; most notably, ponderosa pine (*Pinus ponderosa*) no longer naturally thinned from fire developed dense thickets (Parrish et al. 1996). Improvement in suppression technology resulted in fewer fires escaping containment and an overall increase in ponderosa pine forests (Parrish et al. 1996). The increased pine canopy led to diminished understory productivity and a simplification of community diversity (Progulske 1974, Parrish et al. 1996). The increase in overall forest coverage however, may have increased stalking cover for cougars. With increased European settlement in the Black Hills region, wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) were extirpated and have yet to successfully recolonize the Black Hills (Higgins et al. 2000). Lack of interspecific competition was likely advantageous to cougars in the Black Hills, putting them as the dominant carnivore in the predator guild. Finally, market hunting of ungulates in the Black Hills was ended by the early 1900s and state management allowed ungulate species to increase throughout the Black Hills ecosystem; populations of white-tailed deer
(Odocoileus virginianus) and elk (Cervus elaphus) were at record highs in the Black Hills during the time of our research (Huxoll 2006). The combined interaction of these factors provided conditions that likely promoted population growth of cougars within the Black Hills.

Beginning in 1985, state biologists began recording cougar sightings in South Dakota (Froiland 1990) and estimated that 10-15 resident cougars inhabited the Black Hills (T. Benzon, South Dakota Game, Fish and Parks, person. commun.). Cougar sightings continued to increase and the first intensive field study of cougars in the Black Hills was initiated in 1998 (Fecske 2003), documenting cougar distribution and abundance. Fecske (2003) determined that cougars ranged throughout the Black Hills ecosystem and estimated a resident population of 130 -150 animals. Cougars inhabiting the Black Hills are unique in that they are semi-isolated from other breeding cougar populations. The closest known breeding populations are in the Bighorn Mountains (200 km to the west) and the Laramie Mountain Range (120 km to the southwest; Fecske 2003) of Wyoming. A breeding population of cougars has recently established in the North Dakota Badlands, approximately 180 km to the north of the Black Hills (North Dakota Game and Fish Department 2007).

In 2003, the cougar was removed from the state-threatened species list and classified as a game animal to be managed by the South Dakota Department of Game, Fish and Parks (Fecske 2003, Anderson et al. 2004). Historically, many carnivore species were managed more based on art than science (Cougar Management Guidelines Working Group [CMGWG] 2005). In South Dakota, initial management efforts for
cougars consisted primarily of population-level assessment and removal of problem animals for safety or depredation reasons. As more cougar/human interactions and conflicts arose, intensive research continued with additional animals tracked and more research questions and objectives identified.

The study area for our cougar research encompassed the Black Hills mountain range located in western South Dakota and northeastern Wyoming (Figure 1.1). Primary objectives were to: 1) document cougar survival by sex and age class (i.e., kitten, subadult, and adult) and characterize mortality of an unhunted cougar population, 2) document dispersal movements and assess philopatry of a cougar population semi-isolated from other populations in a region surrounded by atypical cougar habitat, 3) assess the genetic structure of a semi-isolated cougar population, 4) document morphological attributes of a newly recolonized cougar population, and 5) assess population status and document effects of density dependence as they relate to overall population demographics of the cougar population in the Black Hills.

Literature Cited


North Dakota Game and Fish Department. 2007. Status of mountain lion management in
North Dakota. North Dakota Game and Fish Department, Bismarck, North
Dakota, USA.

Parrish, J. B., D. J. Herman, D. J. Reyher. 1996. A Century of Change in Black Hills
Forest and Riparian Ecosystems. United States Forest Service, Agricultural
Experimental Station, United States Department of Agriculture, South Dakota
State University, Brookings, South Dakota.

Progulske, D. R. 1974. Yellow Ore, Yellow Hair, Yellow Pine: A Photographic Study
of a Century of Forest Ecology. Bulletin 616. Agricultural Experimental Station,
South Dakota State University, Brookings.

Roosevelt, T. 1926. Hunting trips of a ranchman, and The wilderness hunter.

Diseases 38:107-114.

Miscellaneous Publication No. 60, University of Kansas Publications, Museum of
Natural History, Lawrence, USA.

Young, S. P., and E. A. Goldman. 1946. The puma: Mysterious American cat. Dover
Publications, Inc. New York, New York, USA.
Figure 1.1-Map of Black Hills study area located in western South Dakota and eastern Wyoming, encompassing approximately 8,400 km². Inset map of study area from Feckse (2003).
CHAPTER 2: SURVIVAL AND MORTALITY CHARACTERISTICS OF AN UNHUNTED COUGAR POPULATION IN THE BLACK HILLS OF SOUTH DAKOTA

Abstract

Understanding survival and mortality characteristics of wild animal populations is important for managing and conserving species. Cougar (*Puma concolor*) populations have expanded in many western areas of the United States, including the Black Hills of South Dakota. Our objectives were to calculate survival and cause-specific mortality of an unhunted cougar population in the Black Hills of South Dakota. The Black Hills are an isolated mountain range located in southwestern South Dakota and eastern Wyoming. We captured and radiocollared cougars from 1999 - 2005 and collected weekly telemetry data to assess survival. We documented known cougar mortality throughout South Dakota in conjunction with the South Dakota Department of Game, Fish and Parks. We captured 35 independent aged cougars (*n* = 15 males; 20 females) for survival analyses. Annual survival of independent adult cougars averaged 0.869 (range: 0.50 - 1.0 annually); no difference (*P* > 0.05) occurred between adult males and females. Subadult males had the lowest survival rate (0.62) of any sex/age class in our study area. Kitten survival was 0.67 based on data from 5 separate litters. We documented 85 mortality events in South Dakota from 1998-2005. Vehicles (32.9%) and depredation removals (21.2%) accounted for most cougar mortalities in the Black Hills, with 85% of mortality being human-induced. Results represent baseline data that will be useful for evaluating effects of future manipulations of this population.
Keywords: cougar, *Puma concolor*, survival, cause-specific mortality, unhunted, Black Hills, South Dakota

Introduction

In recent years management plans for populations of cougars (*Puma concolor*) have come under criticism for lack of a defined scientific basis (Cougar Management Guidelines Working Group, CMGWG 2005); thus, agencies throughout the cougar’s range are improving research and management techniques to develop management scenarios based on the best available science. Primary factors affecting cougar population dynamics and population status are survival, natality, and cause-specific mortality (Ross and Jalkotzky 1992, Lindzey et al. 1994, Lambert et al. 2006) and an accurate assessment of these parameters is essential in order to accurately assess a population. Reliable estimates of cougar survival between sex and age classes allows for a quantitative assessment of population status. Documenting mortality events affecting a cougar population also provides insight into conservation and management scenarios that may be effective depending on objectives (Logan and Sweanor 2001, Anderson and Lindzey 2005, Lambert et al. 2006.)

Previous research on cougar survival and mortality has been conducted throughout the western United States and Canada (Logan et al. 1986, Lindzey et al. 1988, Ross and Jalkotzky 1992, Lindzey et al. 1994, Spreadbury et al. 1996, Cunningham et al. 2001, and Lambert et al. 2006). Results of studies found varying survival rates for cougars along with differential cause-specific mortality, especially between hunted (Logan et al. 1986, Ross and Jalkotzky 1992) and unhunted (Lindzey et al. 1994, Logan
and Sweanor 2001) populations. The primary source of mortality in hunted populations was generally attributed to sport hunting, whereas in unhunted populations intraspecific strife was the primary source of mortality (Logan and Sweanor 2001). The Florida panther represents an exception to the mortality pattern documented for western cougars; primary causes of mortality were attributed to vehicular trauma followed by intraspecific strife (Taylor et al. 2002).

The cougar population in the Black Hills of southwestern South Dakota and eastern Wyoming is unique in that it is semi-isolated from western cougar populations (not contiguously connected), on the eastern edge of current cougar range (Cougar Network 2007), and that it has naturally recovered from near extirpation to become a viable breeding population (Fecske 2003). Along these lines, prior to 2005, the population in South Dakota was unharvested; harvest began on the Wyoming side of the Black Hills in 1999 (Anderson 2005). In South Dakota, prior to initiation of harvest, animals deemed problematic due to depredation or human safety risk were removed from the population by the South Dakota Department of Game, Fish and Parks.

The Black Hills National Forest (BHNF) is highly developed and one of the most heavily roaded national forests, with 13,411 km of inventoried roads within and adjacent to the BHNF boundary (United States Department of Agriculture [USDA] Forest Service 2007). Our objectives were to document and assess survival of cougars captured within the Black Hills along with determining mortality characteristics and cause-specific mortality. We hypothesized that the highly developed nature of the Black Hills, combined with an increasing cougar population would result in a high proportion of
human-induced mortality despite the fact that the population was not actively harvested
during our field work.

Study Area

The Black Hills are located in west-central South Dakota and northeastern
Wyoming, represent the eastern most extension of the Rocky Mountains, and correspond
in age to the oldest mountains in North America (Froiland 1990). Our study area
encompassed the Black Hills, covering approximately 8,400 km² (Fecske et al. 2002;
Figure 1.1). The Black Hills are a dome-shaped structure, sloping more steeply to the
east than to the west with maximum elevation of 2,207 m above mean sea level (Froiland
1990). Soils of the Black Hills are within the gray wooded soil region, which is unique
for South Dakota (Froiland 1990). These soils were largely developed under timber in
dry sub-humid to humid climate and are derived from limestone, sandstone, and local
alluvium from igneous and metamorphic rocks (Froiland 1990). The Black Hills
ecosystem is composed of four distinct vegetation complexes: 1) Rocky Mountain
coniferous forest, 2) Northern coniferous forest, 3) Grassland complex, and 4) Deciduous
complex. Forest cover in the Black Hills is predominantly ponderosa pine (Pinus
ponderosa) with codominants of white spruce (Picea glauca) and quaking aspen
(Populus tremuloides). The Black Hills are an isolated mountain range, being completely
surrounded by the Northern Great Plains.

Primary prey species available to cougars on the study area included white-tailed
deer (Odocoileus virginianus), mule deer (O. hemionus), elk (Cervus elaphus), bighorn
sheep (Ovis canadensis), mountain goat (Oreamnos americanus), and porcupine
(Erethizon dorsatum), along with small mammals and domestic livestock species. The predator guild of the Black Hills included coyote (Canis latrans) and bobcat (Lynx rufus); with gray wolf (Canis lupus), grizzly bear (Ursus arctos), and black bear (Ursus americanus) extirpated from the region around the late 1800s to early 1900s (Froiland 1990).

Methods

We captured cougars in 1999 - 2005 throughout the Black Hills study area primarily with the aid of hounds. We were opportunistic in our capture techniques using walk-in live traps, foot-hold snares (Logan et al. 1999), and leg-hold traps with offset jaws when applicable. We immobilized cougars using a telazol (2.2 mg/lb) and xylazine (0.45 mg/lb) mixture (Kreeger 1996) based on live animal body weight estimated by the capture crew. Cougars were aged by tooth wear and pelage characteristics (Anderson and Lindzey 2000), and animals > 10 months old were fitted with very high frequency (VHF) radio-transmitters (Telonics, Inc., Mesa, Arizona, USA). Immobilized cougars were reversed (0.125 mg/kg) and released on site and observed from a distance to assure safe recovery. We captured kittens (< 2 months old) of radio-marked females by hand to determine age of independence and dispersal. Kittens were fitted with expandable VHF radio-collars (Telonics, Inc., Mesa, Arizona, USA). Kittens > 3-months old were fitted with eartag radio-transmitters then recaptured when ≥ 10-months old and fitted with adult transmitters to replace eartag transmitters. All captured cougars were fitted with numbered ear tags regardless of age or sex.
We located study animals weekly via aerial telemetry from a fixed-wing aircraft, and used ground triangulation and visual observation to relocate animals between flights. The high road density of the Black Hills allowed adequate access for ground triangulation throughout the majority of the study area. We used visual observation and track counts to assess kitten survival. We classified animals as: kitten--still dependent with mother, subadult--independent from mother but not part of the breeding population (usually < 2.5-yrs old), and adult--an individual occupying a resident home-range within the study area (generally ≥ 2.5-years old). We used Kaplan-Meier procedures to calculate annual survival ($S$) between sex and age classes allowing for staggered entry and censorship (Pollock et al. 1989). Generally, as animals left the population they were censored; however, due to the high percentage of subadult males that leave cougar populations we calculated survivorship while they were transient within the study area. Animals leaving the population were censored when we lost contact with them, but we wanted to calculate vulnerability to mortality while dispersing within the study area regardless of animal fate after dispersing from the Black Hills.

We used two techniques for assessing mortality. We documented cause-specific mortality of radio-collared animals continuously throughout the project. When a mortality signal of a radio-marked cougar was encountered, we immediately retrieved the collar and determined the cause of the mortality signal. In instances of mortality, we conducted a thorough examination of the carcass along with surveying the surrounding area within a 100-m radius of the mortality site. In cases where mortality could not be determined on site from gross observation, we transported the carcass to South Dakota
State University or South Dakota Department of Game, Fish and Parks (SDGFP) and conducted a necropsy to determine cause of death. Along with determining mortality from marked individuals, we documented any mortality events of cougars that occurred within the Black Hills, in conjunction with SDGFP. If cause-specific mortality could not be determined from gross examination of the cougar carcass, the mortality site was surveyed to collect information that would assist with determining cause of mortality using the same techniques as we used with radio marked individuals. All carcasses were necropsied (cause-specific and general mortalities) to determine cause of death, along with providing age and gender information for the individual. Known cougar mortalities were recorded beginning in 1998 in South Dakota, which resulted in trend data that related deaths/year and cause of death. We used Kruskall-Wallis analyses to compare mortality events between years. In particular, we wanted to document changes in survival rates and causes of mortality through time.

Results

Survival

We captured 35 cougars for survival analyses (n = 15 males and 20 females). We tracked males an average of 600.8 days (range = 53 - 2440 days) and females an average of 599.5 days (range = 50 - 2081 days). Annual female and male survival ranged from 0.50-1.0 from 2000 - 2005 (Table 2.1). Mean annual male (0.82; SE = 0.07) and female (0.85; SE = 0.08) survival of independent cougars did not differ (t = -0.38, df = 5, P = 0.83). We documented 5 mortality events of radio-marked females (Table 2.1). Of the 15 males tracked, 8 were subadult males and 7 were resident adult males. No subadult
males were recruited into the population primarily due to dispersal (see Chapter 3), but we did track survival of cougars prior to their dispersal. Three subadult males died (2 vehicle trauma, 1 removal) while in the Black Hills study area, with the remaining 5 dispersing from the Black Hills ($S = 0.62$). We tracked subadult males an average of 155.8 days while in the study area. Three adult male cougars died during the study; two of the resident males captured were tracked > 2,300 days and were still alive at the end of the study.

We captured 15 kittens from 5 unique litters. Litter size averaged 3 kittens/litter (range = 2 - 4), with a 5:1 male to female sex ratio. One kitten died from unknown causes and one litter ($n = 4$) died due to infanticide. Remaining litters and marked animals reached independence ($S = 0.67$). Although we did document additional litters and captured other kittens, we experienced radio failure and reported our estimates based only on known fates.

*Cause-specific Mortality (Radio-marked cougars)*

We documented 13 mortalities of marked cougars from 1999 - 2005. Depredation removal ($n = 3$) and illegal kill ($n = 3$) accounted for the highest number of radioed cougar mortalities. Vehicular trauma ($n = 2$) and intraspecific strife ($n = 2$) accounted for 30.8% of mortality. We documented infanticide of one marked animal, with the other three litters succumbing to infanticide. We documented cause-specific mortality from drowning ($n = 1$) and forest fire ($n = 1$; Fecske et al. 2003). Natural mortality accounted for 38.4 % of total cause-specific mortality from radiomarked cougars.

*Mortality Characteristics (All documented mortality)*
We documented 81 cougar mortality events in the Black Hills in 1998 - 2005. Death associated with vehicular trauma was the primary mortality source \((n = 28)\), followed by SDGFP departmental removal for \((n = 18)\), incidental snaring \((n = 8)\), intraspecific strife \((n = 6)\) from interactions or infanticide, and illegal killing \((n = 5)\) (Figure 2.1). We documented 8 mortality events due to unknown causes. The number of mortality events recorded annually increased from 1998 to 2005 (Figure 2.2). Overall, 85% of cougar mortality in the Black Hills was human-induced.

The average age of death for cougars in South Dakota was 2.6 years and we found no difference \((P > 0.50)\) between age at death of male and female cougars. A higher number of males \((n = 45)\) died compared to females \((n = 32)\). More males \((n = 15)\) than females \((n = 3)\) were removed due to depredation or human safety reasons (Figure 2.3). Vehicular trauma was a major source of mortality for both male and female cougars (Figure 2.3). We recorded 3 cases of emaciation that ultimately caused mortality.

Of the 77 mortality events attributed to a specific cause, 12 were considered natural mortality \((15.6 \%)\), with the remaining events \((n = 65; 84.4 \%)\) considered human-induced or human-related causes of mortality. Natural mortality was primarily due to interaction with other lions or emaciation.

Discussion

Survival rates documented in the Black Hills were within the range of those found in most western cougar populations (Lindzey et al. 1988, Logan et al. 1986, Spreadbury et al. 1992). Logan et al. (2001) noted higher annual survival in an unhunted population of cougars in the southwestern United States. We noted variable annual survival \((0.50 - \)
1.0) during our study. We also documented similar kitten survival to that of other unhunted populations (Lindzey 1987, Logan et al. 2001). With the exception of one unknown cause of kitten death, all kitten mortality was attributed to death of an entire litter \((n = 4)\) as a result of infanticide. Although we noted other litters throughout the course of the study based on visual observations and tracks, we did not include these observations in our analyses as they may have been biased by the fact that we did not track litters from birth or through independence. Average cougar litter size in the Black Hills was higher than those documented for other populations (Pierce and Bleich 2003), and sex ratio of cougars was highly skewed towards males, which may be a result of population saturation and density dependence (Julliard 2000).

Intraspecific strife generally assumes a primary role in mortality of unhunted cougar populations (Logan and Sweanor 2001). Although we documented several instances of mortality due to interaction between cougars, it was not one of the more significant causes of mortality affecting cougar survival in the Black Hills. Although this population was protected from hunting, nearly 85% of cougar mortality was attributed to human influences. This high human-induced mortality was much more characteristic of hunted cougar populations (Logan et al. 1986, Anderson et al. 1992, Ross and Jalkotzy 1992, Lambert et al. 2006). Mortality associated with vehicular trauma is a significant source of mortality in the Florida panther (35%, Taylor et al. 2002), which was similar to the rate documented for cougars in South Dakota. Vehicular trauma also was documented in a nonhunted cougar population in British Columbia (Spreadbury et al. 1996). The Florida panther is susceptible to vehicular mortality due to high human
population, fragmentation, and a boundary of unsuitable habitat that deters transient panthers from leaving the area and increases susceptibility to vehicular mortality (Maehr et al. 2002, Taylor et al. 2002). In British Columbia, vehicular mortality was mainly attributed to traffic associated with mining operations; where mining traffic was high during periods when cougars were most active. As we noted earlier, the Black Hills National Forest has one of the highest road densities (USDA Forest Service 2007) of any national forest, along with a relatively high human density compared to remote wilderness areas of most western cougar populations. Tourism is one of the largest industries to the Black Hills, with traffic increasing to the maximum from May through September (South Dakota Department of Transportation [SDDOT] 2007). Transient cougars are continually on the move (Thompson and Jenks 2005); therefore, they are more susceptible to mortality events when crossing major highways and interstates. Although annual traffic has not increased significantly over the past decade (approximately 1% increase in traffic/year [SDDOT 2007]), the number of cougar mortalities due to vehicle trauma has increased.

The second major cause of mortality to Black Hills cougars was removal for depredation or public safety concerns. Some wildlife agencies use lethal removal of problem animals as a management method. Removal of problem animals is a significant source of mortality for cougars in southeastern Arizona (Cunningham et al. 2001) and in the Uncompahgre Plateau of Utah (Anderson et al. 1992). Depredation removal is the primary source of human-related mortality in California, which does not allow sport
harvest (Orlando and Demment 2005); > 100 animals have been removed annually since 1999 (Updike 2005).

When comparing cause-specific mortality of marked cougars to total mortality we noted similar rates of depredation removals. The small number \( n = 13 \) of mortalities documented from marked cougars warrants caution of interpretation, but it is important to note that we documented higher rates of mortality attributed to illegal kill and slightly higher rates of interaction/infanticide of marked cougars. Even if diligently documenting known cougar mortality in a particular region, it is quite possible that instances of illegal killing and intraspecific strife go unnoticed and could cause an underestimation of total survival and mortality. Of the three illegal kills of radiomarked cougars, two individuals would not have been found if animals were not radio collared. In our study, mortalities due to intraspecific strife between males would have been included in known mortalities whether or not the animals had been marked. Infanticides almost surely go unnoticed in some instances, which further supports the importance of gaining baseline knowledge on cougar population survival for all age classes when developing adaptive management plans.

“Anomalous” mortalities we documented are also worthy of discussion. Emaciation is generally a sign of population saturation and litter abandonment. While drowning is rare, it has been documented in other cougar populations (Cunningham et al. 2001). The mortality event attributed to forest fire also was considered a rare event (Fecske et al. 2004). While instances of mortality such as these most likely do not account for significant mortality episodes in cougar populations, it is important to
document their contribution to cumulative mortality especially when dealing with cryptic
animals and/or large carnivores at relatively low densities. These rare instances of
mortality provide an index of cumulative annual mortality and are useful for population
monitoring and modeling.

Based on factors such as the semi-isolated nature of the region coupled with
habitat encroachment and fragmentation from human inhabitation, it appears the
population is more susceptible to human-induced mortality especially in the forms of
vehicular trauma and removal of problem animals when compared to more remote cougar
populations. Although a significant amount of high quality habitat (6,723 km$^2$) is readily
available for cougars in the Black Hills (Fecske 2003), much of it occurs in close
proximity to towns and cities. The most suitable habitat for cougars is also heavily
dissected by the > 13,350 km of roads within the region, with development occurring at a
rapid rate throughout the Black Hills ecosystem (USDA 2007). Despite problems
associated with cougar/human coexistence, cougar survival in the Black Hills is relatively
high and the population appears to be adapting to human presence, with humans
somewhat reluctantly accepting the omnipresence of cougars throughout the ecosystem.

Management Implications

We investigated population demographics of the cougar population in the Black
Hills. During the course of our study, vehicular interactions and removal of problem
animals were the primary sources of mortality in the South Dakota portion of the Black
Hills. Vehicle related mortality is a nationwide issue for many ungulate species causing
significant mortality and financial damage (Conover 1995). Wildlife agencies have been
working on solutions to the vehicle-wildlife interaction question (Clevenger and Waltho 2005) with mixed results. While use of fencing can effectively alter crossing patterns in certain species (Clevenger et al. 2001), we do not believe this is a viable option for cougars inhabiting the Black Hills. Long narrow crossing structures in close proximity to forested habitat such as highway underpasses were the most preferred structures chosen for cougars (Clevenger and Waltho 2005). While the vehicle-mortality of cougars in the Black Hills does not appear to have an overall detrimental effect on the population, we suggest continuing annual assessments of cougar mortality to determine if a future need may exist to develop road crossing structures decrease loss, especially in areas where multiple cougar deaths due to vehicles have been documented.

Insight into cumulative mortality, especially in cougar populations cohabiting areas with humans, is essential for assessment of population demographics. Documentation of known mortality events in a particular region is helpful in assessing causes of mortality along with providing annual indices and insight into survival. Baseline survival data is important for allowing managers to assess population structure and variation occurring due to changes in habitat, human encroachment, or harvest changes. Documentation of cause-specific mortality of marked animals provides further insight into mortality events that otherwise may go unnoticed, especially instances of illegal kills and intraspecific strife, providing valuable indices for population monitoring and modeling.
Literature Cited


Froiland, S. G. 1990. Natural History of the Black Hills and Badlands. The Center for Western Studies, Augustana College, Sioux Falls, South Dakota, USA.


North Dakota Game and Fish Department. 2007. Status of mountain lion management in North Dakota. North Dakota Game and Fish Department, Bismarck, North Dakota, USA.


South Dakota Department of Transportation. 2007. Automatic Traffic Recorder Data. Division of Planning and Engineering, Transportation Inventory Management. Pierre, South Dakota, USA.


Table 2.1. Annual survival estimates \( (S_i) \) for independent aged cougars in the Black Hills of South Dakota, 1999-2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males (N)</th>
<th>Annual Male ( S_i )</th>
<th>Females (N)</th>
<th>Annual Female ( S_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>4</td>
<td>0.75</td>
<td>0</td>
<td>N/A</td>
</tr>
<tr>
<td>2000</td>
<td>3</td>
<td>0.67</td>
<td>4</td>
<td>0.75</td>
</tr>
<tr>
<td>2001</td>
<td>2</td>
<td>1.00</td>
<td>3</td>
<td>1.00</td>
</tr>
<tr>
<td>2002</td>
<td>3</td>
<td>1.00</td>
<td>4</td>
<td>0.50</td>
</tr>
<tr>
<td>2003</td>
<td>7</td>
<td>1.00</td>
<td>5</td>
<td>1.00</td>
</tr>
<tr>
<td>2004</td>
<td>8</td>
<td>0.50</td>
<td>13</td>
<td>0.92</td>
</tr>
<tr>
<td>2005</td>
<td>5</td>
<td>0.80</td>
<td>16</td>
<td>0.94</td>
</tr>
</tbody>
</table>

Mean = 4.57 \( (SE \ 0.07) \) 6.43 \( (SE \ 0.08) \)
Figure 2.1. Breakdown (%) of mortality events \( n = 85 \) documented for cougars in South Dakota, 1998 - 2005.
Figure 2.2. Yearly breakdown of annual cougar mortality events documented in South Dakota, 1998 - 2005.
Figure 2.3. Comparison between male and female cougar mortalities in the Black Hills of South Dakota, 1998 - 2005; (categories represent primary sources of mortality).
CHAPTER 3: DISPERSAL MOVEMENTS OF SUBADULT COUGARS FROM THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING: THE NOTIONS OF RANGE EDGE, RANGE EXPANSION, AND RECOLONIZATION.

ABSTRACT

Dispersal plays a vital role in cougar (*Puma concolor*) population ecology, creating genetic viability and maintaining gene flow between populations. The cougar population in the Black Hills is at the edge of the species’ range in North America and completely surrounded by the Northern Great Plains. Our objective was to document dispersal movements of subadult cougars captured within the Black Hills ecosystem of southwestern South Dakota and eastern Wyoming. Cougars were captured during the winters 2003 - 2006, fitted with VHF radio-transmitters, and monitored weekly. Locations were plotted in ArcGIS and dispersal distances calculated from capture site or natal home-range center point to site of death, last known location, or post-dispersal home-range center point. Kittens were captured from radioed females to document age of independence and dispersal. Twenty-four subadult cougars were captured in the Black Hills (*n* = 14 males, *n* = 10 females). Independence of cougars from females averaged 13.5 months (range = 10 - 16 months) from parturition; dispersal occurred 1-3 months post independence. Males dispersed (Mean = 274.7 km SE 88.3) farther than females (Mean = 48.0 km SE 10.9), with females exhibiting 40% philopatry. No subadult males were recruited into the Black Hills cougar population. We documented several (*n* = 6) long-distance dispersal movements (>200 km) of male cougars and hypothesize that
males making long-distance movements were in search of available mates. Movements documented by our study indicate that range expansion and habitat recolonization are occurring and further suggest agencies need to react proactively to cougar movements and increase public knowledge of cougar ecology in areas where cougars are recolonizing previously occupied habitats.

Keywords: cougar, *Puma concolor*, dispersal, long-distance dispersal, range expansion, repatriation, Black Hills, South Dakota, Wyoming.

Introduction

Dispersal is pivotal to population ecology and dynamics of the cougar (*Puma concolor*) in North America. Dispersal has been defined as the permanent movement away from an individual’s natal home-range/area (Greenwood 1980). Dispersal is a crucial aspect of population demographics facilitating genetic transfer helpful toward maintaining healthy wildlife populations across large landscape-scale levels (Sinclair et al. 2001, Anderson et al 2004). Howard (1960) classified dispersal as innate or environmental. Innate dispersal is considered a predisposition to move beyond the confines of a parental home-range, whereas environmental dispersal is in response to “crowded situations” and density dependence (Howard 1960).

Cougar populations across the western United States have shown interrelatedness and movement among populations (Culver et al. 2000, Sweanor et al. 2000, Anderson et al. 2004), a pattern meeting the definition of a metapopulation. Recent genetic analyses classified all cougars ranging north of Argentina as one interrelated subspecies (*P. c. cougar*; Culver et al. 2000), and it was found that across the Wyoming Basin
geographically separate populations were considered panmictic (Anderson et al. 2004). Dispersal among cougar populations allows for genetic material to be introduced and intermixed between otherwise geographically isolated regions (Sweanor et al. 2000, Logan and Sweanor 2001). As habitat fragmentation increases throughout cougar range, movement among populations remains critical to maintain genetic population viability (Beier 1995, Sinclair et al. 2001).

Cougar populations in the western United States increased in the latter portions of the 1900s (Pierce and Bleich 2003). Within the last decade a noticeable increase in verified cougar presence east of established breeding ranges suggest cougars are recolonizing historic habitat (Cougar Network 2007). As large carnivores extend their current range, increased knowledge of their movements in urban and rural areas is needed to identify conservation and management issues that should be addressed. Our objective was to document dispersal of a semi-isolated cougar population on the eastern edge of known cougar range. We also were interested in documenting and assessing movements of cougars traversing historic areas that may have been devoid of cougars for > 100 years (Thompson et al. 2009).

The cougar population of the Black Hills of South Dakota and Wyoming provides a prime example of a naturally recolonized, semi-isolated cougar population on the edge of current distribution (Cougar Network 2007). We consider cougars in the Black Hills semi-isolated in that they are not contiguously connected to western breeding cougar populations, but emigration is possible (Fecske 2003, Anderson et al. 2004). The Black
The Black Hills are a dome-shaped structure, sloping more steeply to the east than from the west with highest elevation of 2,207m (Froiland 1990). Soils of the Black Hills are identified as the gray wooded soil region, which is unique for South Dakota (Froiland 1990). These soils have largely developed under timber in dry sub-humid to humid climate and are derived from limestone, sandstone, and local alluvium from igneous and metamorphic rocks (Froiland 1990). The Black Hills ecosystem is comprised of four distinct vegetation complexes: 1) Rocky Mountain coniferous forest, 2) Northern
coniferous forest, 3) Grassland complex, and 4) Deciduous complex. Forest cover in the Black Hills is predominantly ponderosa pine (*Pinus ponderosa*) with co-dominants of white spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*).

Primary prey species available on the study area includes: white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*) and porcupine (*Erethizon dorsatum*), along with assorted small mammal species and domestic/livestock species (Higgins et al. 2000). The predator guild of the Black Hills included coyote (*Canis latrans*) and bobcat (*Lynx rufus*); wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*) were extirpated from the region in the late 1800s to early 1900s (Higgins et al. 2000).

**Methods**

We captured cougars from 2003 - 2006 throughout the Black Hills study area primarily with the aid of hounds, as well as opportunistic use of walk-in live traps, foot-hold snares (Logan et al. 1999), and leg-hold traps with offset jaws. We immobilized cougars using a telazol (2.2 mg/lb) and xylazine (0.45 mg/lb) mixture (Kreeger 1996) based on estimated live animal body weight. Captured cougars were aged by tooth wear and pelage characteristics (Anderson and Lindzey 2000), and animals > 10 months old were fitted with adult VHF radiotransmitters (Telonics, Inc., Mesa, Arizona, USA). Immobilized cougars were reversed (0.125 mg/kg), released on site and observed from a distance to assure safe recovery. We captured kittens (< 2 months old) of radio-marked
females to determine age of independence and dispersal. Kittens were fitted with expandable VHF radio-collars (Telonics, Inc., Mesa, Arizona, USA).

We located study animals weekly via aerial telemetry from a fixed-wing aircraft, along with ground triangulation. Animal locations were plotted in ArcGIS (ESRI, Redlands, California, USA). Dispersal distances were calculated from capture point to: site of death, last known location, or home-range center-point if the animal dispersed and successfully established a home-range. In instances where kittens were captured from the den, we used the natal home-range center-point versus the site of capture. Home-ranges were calculated (95% Adaptive Kernel) when necessary using the Home-range Extension in ArcGIS. We chose bandwidths that resulted in the lowest least squares -crossed validation scores (LSCV) to create smoothed home-range polygons (Kie et al. 2002). Cougars that established home-ranges with >5% overlap of natal home-ranges were considered philopatric (Sweanor et al. 2000). If an animal established a home-range within the study area, we considered it successfully recruited into the Black Hills cougar population.

Results

We captured 14 subadult male and 10 subadult female cougars in the Black Hills in 2003 - 2006. We also captured and marked 18 kittens from seven separate litters. Age of independence averaged 13.5 months (range 10 - 16 months) with dispersal occurring 1 - 3 months after animals became independent from mothers. Upon reaching independence, subadult cougars of the same sex generally traveled together for a short time before separating and dispersing solitarily. We noticed no difference in age of
independence or age of dispersal between sexes, but the sex ratio of kittens was highly skewed to males (5:1).

Dispersal of 10 subadult female cougars averaged 48.0 km SE 10.9 (range = 12.3 – 98.6 km). Four (40%) female cougars were philopatric. Several females ($n = 3$) left the study area and established home-ranges or perished. Dispersal of 14 subadult male cougars averaged 274.7 km SE 88.3 (13.3 - 1,067.0 km). No subadult male cougars were recruited into the cougar population in the Black Hills. All males successfully dispersed from their natal areas, but several animals ($n = 6$) died while dispersing before establishing residency. If cougars that died while dispersing were censored, average dispersal rate increased to 450 km SE 123. We documented the longest dispersal movement by a cougar (1,067 km) from the Black Hills to Oklahoma in 2003 (Thompson and Jenks 2005), and 5 other radio-marked cougars moved in excess of 250 km (Figure 3.1).

Five subadult female cougars dispersed > 50 km from natal ranges (Figure 3.2). Female dispersal generally consisted of a movement towards the periphery of the Black Hills (Figure 3.2). Male cougars made similar movements to the periphery, following the edge of the forested regions of the ecosystem before leaving the Black Hills to traverse prairie and agricultural habitats.

**Discussion**

The process of dispersal is important for cougar populations to maintain genetic transfer among populations via immigration or emigration (Sweanor et al. 2000, Anderson et al 2004, Culver et al. 2000), and to reduce strife among competitive
individuals (Logan and Sweanor 2001, Maehr et al. 2002). As seen in other cougar populations, subadult male cougars in the Black Hills dispersed farther than females. Although dispersal rates of our female cougars were comparable to those documented by Sweanor et al. (2000), both male and female cougars dispersed greater distances, on average, than documented in previous research throughout cougar range in North America (Hemker et al. 1984, Logan et al. 1986, Beier 1995, Spreadbury et al. 1996, Sweanor et al. 2000, Logan and Sweanor 2001). Florida panther male and female cougars dispersed on average 68.4 km and 20.3 km respectively with a maximum dispersal of 224.1 km for a subadult male cougar (Maehr et al. 2002). Prior to our results in the Black Hills, the maximum straight-line dispersal distance of a cougar was that of a subadult male dispersing 483 km from the Bighorn Mountains of Wyoming to Colorado (Logan and Sweanor 2000). The maximum documented female cougar dispersal movement occurred in a basin and range landscape of north-central Utah, where a female dispersed 357 linear km, while covering an actual distance of 1,341 km (Stoner et al. 2007).

Age of independence and dispersal was typical for cougars in western North America (Beier 1995, Sweanor et al. 2000, Logan and Sweanor 2001, Pierce and Bleich 2003). We noted that upon reaching independence same sex littermates commingled for 1 - 3 months before disbanding and making solitary dispersal movements. There is a lack of published material related to this phenomenon, and it would be of interest to document the gregarious activities of an otherwise solitary carnivore, especially as it relates to hunting behavior and prey sharing.
We documented longer multiple long-distance movements from male and female cougars than previously found, with many of these animals leaving the Black Hills and crossing regions considered unsuitable for occupation by cougars. Dispersing animals therefore have the ability to emigrate to regions within cougar range that may have otherwise been considered geographically separated. It has been suggested that habitat barriers may limit movements of cougars among populations (McRae et al. 2006) and while this may be evident in areas with higher human habitation, the rural yet heavily fragmented agricultural landscapes crossed by cougars emanating from the Black Hills suggest these types of habitat constraints are not impeding cougar dispersal movements. It would be advantageous to implement global positioning system (GPS) technology on marked individuals to allow for a more indepth assessment of travel rates of dispersing cougars along with identification of potential travel corridors across atypical habitat.

Female cougars elsewhere are generally philopatric (Logan and Sweanor 2001, Pierce and Bleich 2003), but that was not the case in the Black Hills. Movements of females were indicative of resource and intraspecific competition (e.g., environmental dispersal; Howard 1960); rather than establishing a home-range overlapping or adjacent to their natal ranges, several females moved either out of the Black Hills or to the outermost edge of available forested habitat within the study area in order to establish a successful home-range. During our study, females in the Black Hills may have had decreased philopatry compared with other populations due to increased competition between mothers and female offspring (Chapter 6) as well as using dispersal as a mechanism to reduce inbreeding (Logan and Sweanor 2001). Although inbreeding
avoidance has been suggested as a causal factor for male dispersal, it also may facilitate female dispersal in fully occupied habitats. Biek and others (2006) found that intrapopulation female movements were beneficial in maintaining population genetic viability.

Dispersal movements of subadult male cougars in the Black Hills are much farther than previous research has documented (Beier et al. 1995, Logan and Sweanor 2001, Sweanor et al. 2001, Maehr et al. 2002). “Obligate dispersal” has been postulated as a behavior adopted by subadult male cougars to discourage inbreeding, regardless of population density (Logan and Sweanor 2001). Subadult male cougars in the Black Hills dispersing from one end of the study area to the other (> 100km) would generally negate instances of inbreeding based on home-range size and social makeup of resident females; however we failed to document a successful dispersal movement of a male remaining on the study area. While prey species are generally abundant throughout the region, resident males are generally not conducive to allowing new individuals to establish home-ranges within their defended home-range (Logan and Sweanor 2001, Maehr et al. 2002). Competition for mates and resources seems to drive dispersal of subadult male and some female cougars out of the study area into less preferred habitats. More importantly dispersal movements of cougars in the Black Hills may be a function of combined effects of both innate and environmental dispersal (Howard 1960) for both male and female cougars.

Driving factors of dispersal (i.e., inbreeding avoidance, lack of resources/density dependence) would not account for subadult male cougars traveling > 300 km from the
Black Hills. After a cougar left the study area, it was traversing areas devoid of breeding cougar populations for at least 100 years, effectively removing intraspecific competition. Competition for naïve prey (Berger 2001) would be minimal. Unless an animal was successful in reaching regions to the west where bears and wolves occur, the largest source of interspecific competition would come from coyotes and humans. Historically, cougars were noted in riparian regions of the Dakotas and Badlands (Roosevelt 1926, Young and Goldman 1946). Renowned cougar ecologist Maurice Hornocker noted an abundance of cougar habitat in the Midwest (Cougar Network 2007), and recently North Dakota documented 2,706 km² of high quality cougar habitat (NDGFP 2007); suggesting habitat availability is not a limiting factor outside of the Black Hills. We suggest the driving force for these long-distance dispersals is in fact related to breeding activity and creating genetic progeny—mate procurement hypothesis. When subadult male cougars cross regions void of extant populations, they continue to travel until a breeding population is encountered and where they are able to establish residency.

Three long distance dispersers (M17, M19, and M51) successfully reached breeding cougar populations in Montana (M17 and M19) and Wyoming (M51) and upon finding available unoccupied habitat, established home-ranges therein. All three animals were harvested after remaining within their respective home-ranges for at least one year. Other radio-collared cougars dispersing > 200 km were not known to establish home-ranges possibly because they were unable to locate breeding populations. Based on our results, importance of finding an available mate may supercede the effects of habitat and prey availability. This hypothesis may apply to other large North American carnivores
(i.e., bear spp., jaguars *Panthera onca* and wolves) capable of making long-range movements to facilitate recolonization of extirpated populations.

**Management Implications**

Range expansion is a new phenomena occurring for several large carnivores throughout North America (grizzly bears, [Pyare et al 2004]; cougars [Pierce and Bleich 2003]; and wolves [USFWS 2009]). Dispersal of cougars originating in the Black Hills provide evidence that recolonization of cougars is occurring and is further substantiated by increased verified cougar sightings throughout midwestern, southern, and eastern North America (Cougar Network 2007). For example, North Dakota recently documented their first breeding cougar population in the western badlands regions of the state since the 1800s (NDGFD 2007). Although subadult male cougars make most recolonizing movements, female cougars also have dispersed into former cougar ranges. Dispersal of female cougars, especially in a population on the edge of cougar range, constitutes true range expansion and recolonization of the species to former habitats.

With long-range dispersal and recolonization movements in mind, it is essential for wildlife agencies in former cougar ranges throughout North America to be proactive in their dealings with cougars. Pre-emptive management plans, bolstered with public education on cougar ecology and the reappearance of a top-level carnivore, are essential for agencies in order to minimize conflicts that occur between cougars and humans as cougars attempt to recolonize former areas. Range expansion and colonization of cougars are highly contentious topics among the public. We suggest anticipatory management and public education to help avoid future conflicts between transient and
recolonizing cougars and resident humans. Managing agencies must remain transparent in efforts with the public to maintain credibility when dealing with the resurgence of large carnivores. Many agencies managing extant cougar populations have successful education programs already in place, and future collaboration is essential in deterring some of the “cougar hysteria” or “mountain lion madness” (Hamilton 2006) associated with these animals as they return to areas where they have been absent for more than a millennium.

Literature Cited


Froiland, S. G. 1990. Natural History of the Black Hills and Badlands. The Center for Western Studies, Augustana College, Sioux Falls, South Dakota, USA.


North Dakota Game and Fish Department. 2007. Status of mountain lion management in North Dakota. North Dakota Game and Fish Department, Bismarck, North Dakota, USA.


Figure 3.1. Long-distance dispersal movements by subadult male cougars from the Black Hills of South Dakota, 2003 - 2006. (Background image incorporated from Google 2007.)
Figure 3.2. Dispersal movements by subadult female cougars from the Black Hills of South Dakota, 2003 - 2007. (Background image adapted from Google 2007.)
CHAPTER 4: MORPHOLOGICAL CHARACTERISTICS OF COUGARS IN THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING: PREDICTING AGE AND SEX FROM OBTAINABLE FIELD DATA.

Abstract

Despite being classified as one subspecies in North America (*Puma concolor couguar*), cougar populations throughout the continent show variation in morphological characteristics, with a general increase in body size corresponding to increase in latitude (Bergmann’s Rule). The cougar population in the Black Hills is a naturally recolonized cougar population existing at the eastern edge of current cougar range. Our primary objectives were to evaluate overall morphological characteristics of the Black Hills cougar population and to compare them with other cougar populations. We also modeled growth parameters of Black Hills cougars to compare sex and age classes within the population. We tested the predictability of assigning sex and age classifications based on obtainable field data. Body measurements were collected from cougars captured for radiotelemetry studies. We also acquired measurements from cougar mortalities documented in the region. We obtained measurements from 108 cougars (*n* = 48 males, *n* = 55 females). Adult males averaged 63.2 kg (SE 2.0) and 211.9 cm (SE 1.01) in total body length, adult females weighing approximately 67% of males and averaging 195.7 cm in length. Subadult and adult females had similar body measurements, although front pad length and neck circumference differed. Subadult and adult males differed in all body size categories. Subadult males were larger than females. Unlike males, females showed lower correlation among body measurements, which may be associated with
energy demands due to birth, lactation and kitten rearing. Cougars in the Black Hills were comparable in size and weight to cougar populations in western North America. Regression analyses indicated that plantar pad width from front and hind feet were accurate indicators of sex of cougars > 1 years of age. Accurate measurements from reliable tracks may be useful for biologists to assess gender of an unknown cougar; however, age does not correlate as well with track dimensions. We provide a protocol to assess gender from track impressions made from cougars.

Keywords: cougar, *Puma concolor*, morphology, body size, track size, Black Hills, predictive model, South Dakota.

Introduction

During the course of cougar (*Puma concolor*) research involving capture, bodily measurements (e.g., weight, length, and assorted girth measurements) are usually obtained on research animals as well as sex and age information. Studies assessing bodily attributes of western North American cougar populations have ranged from general morphology (i.e., age, weight, length) (Lindzey 1987, Pierce and Bleich 2003) and more in-depth measurements (Young and Goldman 1946, Anderson 1983) to those providing individual animal measurements (Anderson et al. 1992, Logan and Sweanor 2001). Other researchers have focused on modeling population demographics using growth/mass curves and related statistical applications (Maehr and Moore 1992, Laundre and Hernandez 2002). Maehr and Moore (1992) documented differences in growth rates between cougar populations.
Although cougars are currently classified as one subspecies (*P. c. couguar*) in North America (Culver et al. 2000), weights and body measurements vary geographically among populations (Maehr and Moore 1992). A general trend of increasing body size with increasing latitude (Bergmann’s Rule) applies to cougars (Kurten 1993, Iriarte et al. 1990.) Because of spatial variation of body morphology between cougar populations, we were interested in documenting morphological attributes of a recently recolonized cougar population. The cougar population in the Black Hills of western South Dakota and eastern Wyoming was believed to be nearly, if not entirely extirpated from the region by the late 1800s and early 1900s (Higgins et al. 2000), but was naturally reestablished by the latter part of the 20th Century (Feske 2003). In addition to naturally rebounding from near extirpation, the Black Hills cougar population is separated from other breeding populations by > 100 km (Anderson et al. 2004). Our primary objectives were to evaluate overall morphological characteristics of the cougar population in the Black Hills for comparison with other populations. We modeled body measurements and characteristics of cougars by sex and age class. We were also interested in testing the predictability of assigning sex and age classifications based on easily obtainable field data such as track size and length.

**Study Area**

The Black Hills are located in west-central South Dakota and northeastern Wyoming, representing the eastern most extension of the Rocky Mountains and correspond in age to the oldest mountains in North America (Froiland 1990). Our study area encompassed the Black Hills, which covers approximately 8,400 km² of area in
west-central South Dakota (Table 1.1). The Black Hills are a dome-shaped structure, sloping more steeply to the east than to the west with a maximum elevation of 2,207 m above mean sea level (Froiland 1990). Soils of the Black Hills are identified as the Gray Wooded soil region, which is unique for South Dakota (Froiland 1990). These soils were largely developed under timber in dry sub-humid to humid climate and are derived from limestone, sandstone, and local alluvium from igneous and metamorphic rocks (Froiland 1990). The Black Hills ecosystem is comprised of four distinct vegetation complexes: 1) Rocky Mountain Coniferous Forest, 2) Northern Coniferous Forest, 3) Grassland Complex, and 4) Deciduous Complex. Forest cover in the Black Hills is predominantly ponderosa pine (*Pinus ponderosa*) with codominants of white spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*). The Black Hills are an isolated mountain range, being completely surrounded by the Northern Great Plains.

Primary prey species available to cougars in the study area included: white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*) and porcupine (*Erethizon dorsatum*), along with assorted small mammal species and domestic livestock species. The predator guild of the Black Hills included coyote (*Canis latrans*) and bobcat (*Lynx rufus*); with gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), and black bear (*Ursus americanus*) having been extirpated from the region around the late 1800s to early 1900s (Froiland 1990).
Methods

We captured cougars in 2003 - 2005 throughout the Black Hills primarily with the aid of hounds. We were opportunistic in our use of capture techniques; we used walk-in live traps, foot-hold snares (Logan et al. 1999), and leg-hold traps with offset jaws when applicable. We immobilized cougars (to attach radio transmitters) using a telazol (2.2 mg/lb) and xylazine (0.45 mg/lb) cocktail that was administered based on live animal body weight (Kreeger 1996). Cougars were aged by tooth wear and pelage characteristics (Anderson and Lindzey 2000). We weighed animals to the nearest 0.25 kg. Immobilized cougars were released on site and observed from a distance until we were assured of a safe recovery post immobilization. Body measurements on cougars included total length (cm), chest girth (cm), neck girth (cm), front plantar pad length and width (mm), and rear plantar pad length and width (mm; Figure 4.1).

All known cougar mortalities were documented within the study area in conjunction with South Dakota Department of Game Fish and Parks (SDGFP) and Wyoming Game and Fish Department (WGFD). In any instance where intact carcasses were obtained, we collected the same measurements as those obtained on captured cougars. We separated cougars by sex and age classes; male and female cougars ≥ 2.5 yrs old were considered adults, and animals ≤ 2.5 yrs of age considered subadults; we used the same classes for males. Although we collected measurements on all animals and carcasses, we did not include animals < 10 months of age in our analyses because they were not fully developed and we lacked full body measurement data for younger kittens. We calculated mean values for all body measurements for comparison between sex and
age classes, which also allowed for comparisons with other populations. We used t-tests and correlation analyses to compare measurements between ages and sexes. We considered parameters highly correlated when $r^2$ values were $> 0.75$, and set significance levels at $\alpha = 0.05$. We used linear regression to determine relationships among morphological characteristics of cougars in the Black Hills. For regression analyses, we used only animals that were independent or $> 1$ year of age. We used linear regression analyses to assess the predictability of track size collected from plantar pad measurements to predict age and sex of cougars. Track size was chosen as our dependent variable because this measurement can be obtained from any distinct track noted in the field and easily measured. We used protocol similar to Grigione et al. (1999) and Smallwood and Fitzhugh (1995) for plantar track measurements (Figure 4.1). We used only plantar track length and width because the overall track width and length can be subjective depending on the substrate in which the track impression was made, and based on the particular activity of the cougar (i.e., walking, running, or stalking), which could change position of toes relative to overall track size.

Results

We measured 108 cougars, 55 captures and 53 mortalities (Table 4.1). Appendix A lists individual measurements for cougars captured for research purposes. Females had similar body measurements between age classes, with the exception of plantar pad lengths of front feet ($t = 2.2$, $df = 46$, $P = 0.03$) and neck circumference ($t = 2.0$ $df = 46$, $P = 0.05$), both being larger in adult than subadult females (Table 4.1). Body measurements of male cougars differed by age class (Table 4.1), and both adult and
subadult males were larger than females (t = -2.4, df = 49, P = 0.02; Table 4.1.) Adult males averaged 63.2 kg and 211.9 cm in length with subadult males averaging 46.9 kg and 205.9 cm total length. Adult females were approximately 66% the weight of adult males and approximately 17 cm shorter in total length (Table 4.1.)

Weight of males was correlated positively with all other body measurements (r² ≥ 0.75), along with high positive correlation (> 75%) of total length and chest girth with other variables (Table 4.2). Body measurements of female cougars were correlated positively for chest girth and weight (r² = 0.87), neck girth and weight (r² = 0.78), and chest girth and neck girth (r² = 0.86; Table 4.3). We were able to differentiate between males and females based on track size (plantar pad width and length; P < 0.01). Males had larger tracks than females (P < 0.01) along with adult males having larger tracks than subadult males (t = 4.0, df = 45, P = 0.00). We were also able to differentiate between subadult male and adult female front (t = -6.1, df = 52, P = 0.00) and rear pad width (t = -5.8, df = 45, P = 0.00) measurements, with subadult males having larger track dimensions. Regression analyses indicated that track size was a useful tool for predicting male versus female cougar tracks. Front track measurements were successful in predicting weight of females (t = 18.8, P = 0.00) and age (t = -3.6, df = 2, P = 0.001) and weight (t = 18.6, df = 2, P = 0.00) of males.

Discussion

Mean weight and length of cougars in the Black Hills were comparable to cougars found elsewhere in North America (Rocky Mountain West, northwestern United States, western Canada; Lindzey 1987). Mean weights were larger for adult males (63.2 kg) and
females (41.7 kg) in the Black Hills than in California (male = 53.4 kg, female = 35.8 kg; Pierce and Bleich 2003), which is consistent with smaller mean weights of cougars in the southwestern United States and Mexico compared to that in northern latitudes (Anderson 1983). Although geographic variation among populations is somewhat expected, the measurements encountered in Black Hills cougars seem fairly indicative of cougar populations found in the western United States at comparable latitudes (Anderson 1983). We did not encounter any males weighing > 80 kg, which may be related to competition with other cougars and a lack of completely remote areas within the Black Hills ecosystem that may enable an individual to reach such a large weight, prey availability, or a combination of these factors.

We noted sexual dimorphism in body weight and size, which is typical for cougars (Lindzey 1987). Although we documented high correlation between weight and body measurements of male cougars in the Black Hills, the same was not true for female cougars. High variation in female body weight was likely due to the energetic costs associated with birth and care of offspring. Although males defend habitat and females within their territory throughout the annual cycle, they would not encounter the stochastic nature of the energetic costs comparable to those of females during pregnancy, lactation, or while caring for growing offspring. Male cougars have shown a more constant growth/weight curve in males versus females.

Statistical comparison between sex and age classes of Black Hills cougars allowed for classification of unknown specimens based on morphometrics. In cases of where an “unknown” cougar carcass is obtained with indeterminable sex or age by
traditional techniques (i.e., genitalia, tooth wear), ability to collect measurements of variables, such as chest circumference, neck circumference, and length provided the highest predictive ability to discern between both sex and age.

Ability to measure track width and length and differentiate between sex and age is of high importance in that these measurements can be obtained non-invasively either from direct measurement of the track in the field or from track impressions. Nevertheless, condition of the track and type of substrate must be noted to decrease bias of inaccurate measurement of track size. Fresh tracks (< one day old) in sand, mud, or unmelted snow provide the best impressions for accurate measurement, and we suggest measuring all tracks encountered in a particular area from a solitary animal and calculating mean width of front and rear plantar pad measurement to account for any changes in substrate type, foot placement, or measurement error.

Management Implications

Knowledge of body morphology of cougar populations is important to enable comparisons between populations and to classify individuals within populations. We were able to differentiate between track size of subadult and adult male and female cougars by measuring the plantar pads of the front and hind tracks. This could be an effective technique for determining sex and age of a cougar within a particular region. Although overlap in range of measurements occurred, widths of front plantar pads > 57 mm and hind pads > 50 mm were indicative of male cougars; widths of front pads < 54 mm and rear pads < 47 mm corresponded to female cougars with > 90% accuracy. We believe that this measurement technique would be particularly useful in determining sex
and age characteristics of cougars that are documented outside of their current breeding range. In areas where cougars are expanding their range differentiation of sex by track can be important in assessment of the population status as it relates to residency and breeding status. We developed a transparent template (Figure 2) that can be placed directly over a cougar track to aid in determination of sex of unknown animals. Specific cougar age is difficult to estimate based on track size because of overlap between subadult animals. Careful measurement of optimal tracks may be useful in documenting the sex of a cougar especially when found in areas that do not have resident cougar populations.

Literature Cited


Froiland, S. G. 1990. Natural History of the Black Hills and Badlands. The Center for Western Studies, Augustana College, Sioux Falls, South Dakota, USA.


Commentationes Biologicae 63:8pp.


Table 4.1. Morphological characteristics (Mean ± 1 SE) of cougars from the Black Hills of South Dakota and Wyoming, 1998 - 2007.

<table>
<thead>
<tr>
<th></th>
<th>Adult Male (n = 25)</th>
<th>Adult Female (n = 32)</th>
<th>Subadult Male (n = 23)</th>
<th>Subadult Female (n = 27)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (yrs)</td>
<td>5.51 ± 0.57</td>
<td>4.14 ± 0.24</td>
<td>1.92 ± 0.10</td>
<td>1.66 ± 0.05</td>
</tr>
<tr>
<td>Weight (kg)</td>
<td>63.16 ± 1.99ab</td>
<td>41.68 ± 1.01b</td>
<td>46.91 ± 1.42a</td>
<td>36.79 ± 1.15b</td>
</tr>
<tr>
<td>Total Length (cm)</td>
<td>211.89 ± 1.66ab</td>
<td>195.71 ± 2.87b</td>
<td>205.89 ± 2.81a</td>
<td>194.19 ± 1.58b</td>
</tr>
<tr>
<td>Tail Length (cm)</td>
<td>82.02 ± 1.01</td>
<td>76.73 ± 0.85</td>
<td>79.98 ± 1.64</td>
<td>78.87 ± 0.72</td>
</tr>
<tr>
<td>Chest Circ.(cm)</td>
<td>76.16 ± 1.08ab</td>
<td>65.55 ± 0.85b</td>
<td>68.84 ± 1.06a</td>
<td>63.37 ± 1.11b</td>
</tr>
<tr>
<td>Neck Circ. (cm)</td>
<td>41.45 ± 0.67ab</td>
<td>35.36 ± 0.41b</td>
<td>37.70 ± 0.631a</td>
<td>34.07 ± 0.696b</td>
</tr>
<tr>
<td>Front Pad L (mm)</td>
<td>44.44 ± 0.74ab</td>
<td>38.38 ± 0.97b</td>
<td>40.35 ± 0.74a</td>
<td>35.93 ± 0.54b</td>
</tr>
<tr>
<td>Front Pad W (mm)</td>
<td>62.54 ± 0.84ab</td>
<td>52.38 ± 0.76b</td>
<td>58.39 ± 0.60a</td>
<td>52.30 ± 0.54b</td>
</tr>
<tr>
<td>Rear Pad L (mm)</td>
<td>42.08 ± 0.78ab</td>
<td>36.06 ± 0.60b</td>
<td>38.70 ±0.43a</td>
<td>34.63 ± 0.50b</td>
</tr>
<tr>
<td>Rear Pad W (mm)</td>
<td>53.72 ± 0.75ab</td>
<td>45.44 ± 0.56b</td>
<td>50.78 ± 0.67a</td>
<td>46.30 ± 0.64b</td>
</tr>
</tbody>
</table>

* Measurements differed between male age classes (*P* < 0.05)

* Measurements differed between sexes (*P* < 0.05)
Table 4.2. Correlation data for male cougars (>1 yr of age) in the Black Hills of South Dakota and Wyoming. Bold values represent highly correlated variables ($r^2 > 0.75$).

<table>
<thead>
<tr>
<th></th>
<th>Age</th>
<th>Weight</th>
<th>Length</th>
<th>Chest</th>
<th>Neck</th>
<th>FPL</th>
<th>FPW</th>
<th>RPL</th>
<th>RPW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight</td>
<td>0.747</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>0.495</td>
<td>0.805</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chest</td>
<td>0.609</td>
<td>0.919</td>
<td>0.792</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neck</td>
<td>0.585</td>
<td>0.899</td>
<td>0.797</td>
<td>0.941</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FPL</td>
<td>0.625</td>
<td>0.850</td>
<td>0.685</td>
<td>0.827</td>
<td>0.775</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FPW</td>
<td>0.562</td>
<td>0.810</td>
<td>0.791</td>
<td>0.835</td>
<td>0.805</td>
<td>0.773</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RPL</td>
<td>0.550</td>
<td>0.816</td>
<td>0.755</td>
<td>0.847</td>
<td>0.820</td>
<td>0.798</td>
<td>0.849</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>RPW</td>
<td>0.514</td>
<td>0.788</td>
<td>0.739</td>
<td>0.836</td>
<td>0.791</td>
<td>0.788</td>
<td>0.898</td>
<td>0.805</td>
<td>1</td>
</tr>
</tbody>
</table>

Length=Total length
Chest/Neck=Circumference
FPL=Front plantar pad length
FPW=Front plantar pad width
RPL=Rear plantar pad length
RPW=Rear plantar pad width

Table 4.3. Correlation data for female cougars (>1 yr of age) in the Black Hills of South Dakota and Wyoming. Bold values represent highly correlated variables ($r^2 > 0.75$).

<table>
<thead>
<tr>
<th></th>
<th>Age</th>
<th>Weight</th>
<th>Length</th>
<th>Chest</th>
<th>Neck</th>
<th>FPL</th>
<th>FPW</th>
<th>RPL</th>
<th>RPW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight</td>
<td>0.487</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>0.436</td>
<td>0.596</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chest</td>
<td>0.375</td>
<td>0.872</td>
<td>0.450</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neck</td>
<td>0.395</td>
<td>0.778</td>
<td>0.431</td>
<td>0.849</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FPL</td>
<td>0.382</td>
<td>0.379</td>
<td>0.283</td>
<td>0.460</td>
<td>0.459</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FPW</td>
<td>0.007</td>
<td>0.296</td>
<td>0.168</td>
<td>0.276</td>
<td>0.204</td>
<td>-0.148</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RPL</td>
<td>0.231</td>
<td>0.438</td>
<td>0.251</td>
<td>0.457</td>
<td>0.465</td>
<td>0.735</td>
<td>0.062</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>RPW</td>
<td>0.105</td>
<td>0.413</td>
<td>0.299</td>
<td>0.384</td>
<td>0.341</td>
<td>0.376</td>
<td>0.443</td>
<td>0.286</td>
<td>1</td>
</tr>
</tbody>
</table>

Length=Total length
Chest/Neck=Circumference
FPL=Front plantar pad length
FPW=Front plantar pad width
RPL=Rear plantar pad length
RPW=Rear plantar pad width
Figure 4.1. Diagram of plantar pad measurements (mm) for front and hind feet of cougars in the Black Hills of South Dakota and Wyoming, 1998 - 2007.
Figure 4.2. Template to determine sex of unknown cougar track impressions using plantar pad measurements of front and hind feet.
CHAPTER 5: GENETIC STRUCTURE OF A GEOGRAPHICALLY DISJUNCT RECOLONIZED COUGAR POPULATION: THE BLACK HILLS COUGAR

Abstract

Genetic structure of free-ranging wildlife species is an important parameter that contributes to knowledge of population’s demographics. Previous research on genetic structure of cougars suggested that significant movement occurred between most western populations. Habitat and human barriers can affect movement patterns of cougars and deter connectivity between some regions. We assessed the genetic structure of the cougar population in the Black Hills of South Dakota and Wyoming. In addition to evaluating genetic structure, we conducted population assignment tests with nearby cougar populations (North Dakota and Wyoming) based on 20 microsatellite loci. We conducted genetic analyses on 134 cougars from the Black Hills. Although cougars in the Black Hills showed a marginally significant genetic bottleneck, they do not appear to have any deleterious effects from the event. Cougars in South Dakota had an average expected heterozygosity ($H_E$) of 0.542 and observed heterozygosity ($H_O$) of 0.547. Effective population size ($N_e$) of Black Hills cougars was 28 individuals (23 - 39; 95% CL). We were able to successfully assign cougars from South Dakota and North Dakota into separate populations based on data obtained from 20 loci. Based on our results, there is adequate power to discern individual cougars from geographically close (< 200 km) populations using 20 loci, and we recommend that a large-scale genetic database of cougars at an international level be constructed to assess genetic structure and population demographic across the distribution of the species.
Keywords: cougar, *Puma concolor*, genetic structure, microsatellite analysis, Black Hills, South Dakota, Wyoming.

Introduction

Recent improvements in genetic analyses have led to an increased number of studies assessing genetic structure and population demographics of wildlife across North America (O’Brien 1994, Culver et al. 2000, Manel et al. 2003, Miller and Waits 2003, Anderson et al. 2004, Biek et al. 2006). Assessing population structure of wildlife using genetic analyses is an important research tool in that samples can be obtained non-invasively (Pilgrim et al. 2005, Garshelis 2006) or in conjunction with capture of live specimens. Assessing population status with genetic sampling can be important when dealing with rare, threatened, or endangered species (Hedrick 1995, Miller and Waits 2003, Pilgrim et al. 2005), as well as cryptic species, such as cougars (*Puma concolor*).

North American cougars are represented by one species descended from South American cougar emigrants 10,000 - 12,000 years ago (Culver et al. 2000). Although previously believed to be separated into several subspecies inhabiting North America (Young and Goldman 1946), based on Culver et al. (2000) and supported by additional research (Anderson et al 2004, Biek et al. 2003), the North American cougar maintains genetic viability by population immigration/emigration on a large, landscape scale. It has been postulated that factors such as habitat degradation and fragmentation could create barriers deleterious to the genetic flow between seemingly geographically distinct populations (Beier 1995, Ernest et al. 2003). Despite classification of one subspecies inhabiting North America, geographic separation of populations can cause notable
changes in the genetic structure, heterozygosity, and genetic viability, due to the natural processes of genetic drift, which could be exacerbated by isolation and inbreeding (Lacy 1987, Lacy 1997).

The cougar population in the Black Hills of southwestern South Dakota and northeastern Wyoming is on the edge of the established cougar distribution in North America. In addition, cougars in the Black Hills are geographically separated from western breeding populations by at least 120 km of inhospitable (short-grass prairie) cougar habitat (Anderson et al. 2004). Cougars in the Black Hills were nearly if not entirely extirpated from the region by the late 1800s and early 1900s (Fecske 2003) with the population rebounding to a viable breeding population of about 200 individuals by 2005 (Huxoll 2007). Previous data suggested that if extirpation did occur in the Black Hills it was brief and that genetic cohesiveness was maintained, although results were based on a small sample size ($n = 9$; Anderson et al. 2004).

Our objective was to assess the genetic structure of the cougar population in the Black Hills. We documented genetic viability, heterozygosity, relatedness, and effective population size for this cougar population. Telemetry data indicated that a significant proportion of cougars leave the Black Hills ecosystem (Chapter 3), but data as to the amount of immigration are limited. We compared genetic structure of Black Hills cougars to that of other cougar populations (i.e., North Dakota and Wyoming) to compare relatedness and to determine if the population was effected by geographic isolation. Because cougars in the Black Hills were significantly reduced during the early 20th century and due to the population’s semi-isolated state that may make it prone to
inbreeding, an assessment of the genetic structure was essential for understanding population viability.

Study Area

The Black Hills are located in west-central South Dakota and northeastern Wyoming, represent the eastern most extension of the Rocky Mountains, and correspond in age to the oldest mountains in North America (Froiland 1990). Our study area encompassed the Black Hills, covering approximately 8,400 km² (Figure 1.1). The Black Hills are a dome-shaped range, sloping more steeply to the east than west with a maximum elevation of 2,207 m (Froiland 1990). Soils of the Black Hills were identified as the Gray Wooded soil region, which is unique for South Dakota (Froiland 1990). These soils have largely developed under timber in dry sub-humid to humid climate and are derived from limestone, sandstone, and local alluvium from igneous and metamorphic rocks (Froiland 1990). The Black Hills ecosystem is comprised of four distinct vegetation complexes: 1) Rocky Mountain coniferous forest, 2) Northern coniferous forest, 3) Grassland complex, and 4) Deciduous complex. Forest cover in the Black Hills is predominantly ponderosa pine (*Pinus ponderosa*) with co-dominants of white spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*). The Black Hills are an isolated mountain range, being completely surrounded by the Northern Great Plains.

Primary prey species of cougars available in the study area included: white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*) and porcupine (*Erethizon dorsatum*), along with assorted small mammal species and domestic/livestock
species (Higgins et al. 2000). The predator guild of the Black Hills included coyote 
(Canis latrans) and bobcat (Lynx rufus) with wolves (Canis lupus), grizzly bears (Ursus 
arctos), and black bears (U. americanus) extirpated from the region around the late 1800s 
to early 1900s (Higgins et al. 2000).

Methods

We captured cougars in 2003 - 2006 throughout the study area as part of an 
going ecology study in the Black Hills ecosystem. Cougars were primarily 
captured with the aid of hounds. However, we opportunistically captured cougars using 
walk-in live traps, foot-hold snares (Logan et al. 1999), and leg-hold traps with offset 
jaws. All captured cougars were immobilized and blood was extracted for genetic 
analyses on site. In situations where blood extraction was unattainable, we collected hair 
samples for analysis. Along with capture efforts, all cougar mortalities throughout the 
state of South Dakota, including harvested specimens, were recorded in conjunction with 
the South Dakota Department of Game, Fish and Parks (SDGFP) and tissue samples 
obtained for genetic analyses. For carcasses in which the blood was hemolized, a 15 mm 
X 15 mm piece of muscle tissue was removed from the inside of the right rear leg. A tuft 
of 20 - 30 hairs was obtained from each captured cougar or carcass and used to obtain 
deoxyribonucleic acid (DNA) in the event that tissue or blood analyses failed. We 
collaborated with North Dakota Game and Fish and Wyoming Game and Fish 
departments to compare genetic diversity between regions and to conduct population 
assignment tests. DNA and genetic analyses were conducted at the Conservation
Genetics Laboratory, United States Forest Service Rocky Mountain Research Station, Missoula, Montana.

Genomic DNA from tissue and blood samples was extracted with the Dneasy Tissue Kit (Qiagen Inc., Valencia, CA). DNA from hair samples also was extracted with the Dneasy Tissue Kit with modifications outlined by Mills et al. (2000). Samples were analyzed using 20 microsatellite markers (Table 1) (Menotti-Raymond and O’Brien 1995, Menotti-Raymond et al. 1999). Polymerase chain reaction (PCR) volumes (10μl) contained 1.0-3.0μl DNA, 1x reaction buffer (Applied Biosystems, Foster City, CA), 2.0 mM MgC12, 200μM of each dNTP, 1μM reverse primer, 1μM dye-labeled forward primer, 1.5 mg/ml BSA, and 1U Taq polymerase (Applied Biosystems, Foster City, California). The PCR cycling profiles were conducted according to published references and PCR products were run in a 6.5% acrylamide gel and visualized on a LI-COR DNA analyzer (LI-COR Biotechnology, Lincoln NE). Descriptive statistics for the microsatellite results (observed heterozygosity ($H_o$), expected heterozygosity ($H_E$), and $F$ statistics) were calculated using GENALEX (Peakall and Smouse 2006) and GENEPOP (Raymond and Rousset 1995) software programs. Effective population size estimates were calculated using an approximate Bayesian computation (Tallmon et al. 2004, Tallmon et al. 2007). Program ONESAMP (Tallmon et al. 2007) approximates $N_e$ from a single sample of microsatellite data. Based on our specifications, the program created 50,000 simulated populations, and an effective population size was chosen for each population from a uniform random number between the lower and upper $N_e$ (Tallmon et al. 2007). Each generated population is assumed to come from a population with an
initial level of genetic variation determined by the product of its historic effective size and the mutation rate ($4N_{eu}$) (Tallmon et al. 2007).

Results

We analyzed 134 cougars from the Black Hills at 20 loci (Table 5.1). We compared samples from the Black Hills to 18 individual cougars from North Dakota based on 20 loci to assess genetic structure and conduct population assignment tests between populations. We also performed analyses comparing cougar populations in North and South Dakota populations to the cougar database from Wyoming (Anderson et al. 2005), based on 8 loci. There were an average of 4.3 alleles per locus and 86 alleles for cougars in the Black Hills. South Dakota cougars had an average $H_E$ of 0.542 and an average $H_O$ of 0.547 (Table 5.2). Effective population size ($N_e$) of cougars in the Black Hills was 27.9 animals (22.65 - 38.97; 95% CL)

Cougars in the Black Hills had higher genetic variation than those in North Dakota. Both populations had alleles unique to each population (SD: $n = 26$; ND: $n = 6$), and each population showed a marginally significant genetic bottleneck using a two-phase evolutionary model (SD: $p = 0.02$; ND: $p = 0.07$). Use of 20 loci resulted in an $F_{ST}$ of 0.05 between cougars from Black Hills and North Dakota, along with allowing fine scale resolution of population membership using assignment tests (Table 5.3). Two of 18 individuals from the North Dakota samples were assigned to the Black Hills using both allele frequency and Bayesian population assignment techniques (Table 5.3). Based on comparisons using only 8 loci, cougars from the Black Hills were more closely related to cougars in Wyoming ($F_{ST} = 0.024$) than North Dakota ($F_{ST} = 0.043$).
Discussion

Despite a population bottleneck that occurred during the early 20th century, cougars in the Black Hills have maintained genetic viability based on genetic analyses at 20 loci. Observed and expected heterozygosity levels were similar to cougar populations in North Yellowstone and western North American (Walker et al. 2000, Anderson et al. 2004, Biek et al. 2005, Mcrae et al. 2005) and higher than $H_O$ levels found in Utah (Table 5.4). Observed and expected heterozygosity are population level assessments of allelic diversity based on the Hardy-Weinberg (H-W) equilibrium (Mills 2007), where allele and genotype frequencies would remain constant over time if unaffected by natural selection, genetic drift, mutation, and gene flow. $H_E$ is that expected under H-W equilibrium, where $H_O$ is the actual proportion of heterozygous individuals average across loci (Mills 2007). Table 5.4 portrays a comparison of observed heterozygosity levels for cougars in the Black Hills with other North American cougar populations and carnivore species throughout the world.

Our results support conclusions by Anderson et al. (2004) suggesting dispersal occurs between the Black Hills and other cougar populations in Wyoming, allowing sufficient genetic movement between populations and negating otherwise deleterious alleles from inbreeding. No clinical signs of inbreeding (i.e., crooked tails, cowlics, cryptorchidism) have been noted in the Black Hills. In addition to immigration, female dispersal movements within the Black Hills (see Chapter 3) may further increase genetic structure and heterozygosity for the cougar population in the Black Hills. In the Greater Yellowstone Ecosystem, Biek and colleagues (2006) suggested that female cougars made
adequate dispersal movements within populations to negate instances of inbreeding (i.e., sibling and offspring mating), despite their generally philopatric nature. Our documentation of female cougars dispersing from the natal area (Chapter 3) in the Black Hills further supports conclusions reported by Biek et al. (2006).

Effective population size of cougars from the Black Hills is lower than reported for some cougar populations. Utah reported an effective population size of 571 individuals based on a population estimate of 3,000 - 4,000 individuals (Sinclair et al. 2001). $N_e$ estimates from Wyoming averaged approximately 2,500 individuals for the statewide cougar population (Anderson et al. 2004). In comparison, $N_e$ for the Florida panther was estimated at 20 - 40 (Hedrick 1995). Generally, $N_e$ is much smaller and somewhat proportional to the total population size, and has been estimated to be as minimal as 10% of local census population size (Frankham 1995). Population estimates of Black Hills cougars ranged from 200 - 220 individuals during the period when samples were collected for genetic analyses (Huxoll 2006). Periodic assessment of effective population size as it relates to overall population size could assist in detecting deleterious population effects associated with a reduction in $N_e$ through time (Schwartz et al. 1998).

We were able to successfully assign population status to cougars from North and South Dakota using 20 loci. Two cougars from North Dakota were assigned to the Black Hills population, suggesting that these animals emigrated from the Black Hills and were either transient or resident cougars in the North Dakota population when samples were collected. We have documented cougars dispersing from the Black Hills to North Dakota, Wyoming, Nebraska, Minnesota, Montana, and Oklahoma (Thompson and Jenks
2005). It is possible that cougars from the Black Hills originally colonized the North Dakota Badlands; however, our results suggest there has either been immigration to North Dakota from other populations, associated genetic drift within, or a combination of both factors that allow differentiation between the geographically close populations in the Dakotas. Based on 8 loci, Wyoming cougar populations were considered to be one panmictic population (Anderson et al. 2004). It may be of interest to revisit previous research with 20 loci to assess population structure and determine if population assignment tests would provide evidence for separation among geographic ranges throughout Wyoming as well as in comparison with Dakota cougars.

Management Implications

Despite being separated from other breeding cougar populations by ≥ 120 km of atypical cougar habitat, results suggest the level of immigration to the Black Hills was sufficient to maintain genetic viability of the population. Samples from the cougar population of the Black Hills were obtained when the population was initially reaching carrying capacity or a few years after population saturation had occurred (Chapter 6). We suggest continued genetic monitoring of cougars in the Black Hills relative to change in population size and density to detect fluctuations in genetic structure. Tissue samples could be obtained from known mortalities throughout the Black Hills to conduct genetic structure analyses every 3-5 years to monitor genetic viability of the cougar population of the Black Hills.

There was adequate power to discern individual cougars from North and South Dakota, along with power to conduct a more formal landscape genetic analysis to assess
whether landscape features enhance or impede movements. A large-scale database of geographically distinct cougar populations could in theory be constructed for North American cougars. With a comparative database of known breeding cougar populations, it would be possible to assign recolonizing cougars to particular populations and give better insight into possible dispersal linkage areas and the importance of certain source cougar populations. It would also serve as an important tool for comparing genetic structure between cougars found in fragmented landscape habitats with those in more contiguous habitats to discern if barrier effects are affecting genetic transfer between populations. Large-scale databases also would provide agencies with another tool for rigorous assessment of managed cougar populations. Cougars do not remain within agency boundaries (Thompson and Jenks 2005, Stoner et al. 2007) and assessing population structure at landscape levels would help agencies with future collaboration for long-term conservation and management of cougars throughout North America.

Literature Cited


Froiland, S. G. 1990. Natural History of the Black Hills and Badlands. The Center for Western Studies, Augustana College, Sioux Falls, South Dakota, USA.


differentiation and hybridization in North American wolflike canids, revealed by
analysis of microsatellite loci. Molecular Biology and Evolution 11:553-570.


Spong, G., M. Johansson, and M. Bjorklund. 2000. High genetic variation in leopards
indicates large and long-term stable effective population size. Molecular Ecology
9:17731782.

Stoner, D. C., W. R. Rieth, M. L. Wolfe, M. B. Mecham, and A. Neville. 2007. Long-
distance dispersal of a female cougar in a basin and range landscape. Journal of

new effective population size estimator based on approximate Bayesian

program to estimate effective population size using approximate Bayesian
computation. Molecular Ecology Resources 8:299-301.

biologists: A review of applications and recommendations for accurate data

Microsatellite variation in two populations of mountain lions (Puma concolor) in Texas. The Southwestern Naturalist 45:196-203.

### Table 5.1. Genetic variability by locus of samples taken from South Dakota (SD) and North Dakota (ND) cougars.

<table>
<thead>
<tr>
<th>Locus</th>
<th>N</th>
<th>Alleles</th>
<th>Effective Alleles*</th>
<th>H&lt;sub&gt;O&lt;/sub&gt;</th>
<th>H&lt;sub&gt;E&lt;/sub&gt;</th>
<th>F&lt;sub&gt;IS&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SD</td>
<td>ND</td>
<td></td>
<td>SD</td>
<td>ND</td>
<td>SD</td>
</tr>
<tr>
<td>Fca43</td>
<td>134</td>
<td>18</td>
<td>5 2</td>
<td>1.92</td>
<td>1.60</td>
<td>0.50</td>
</tr>
<tr>
<td>Fca57</td>
<td>133</td>
<td>18</td>
<td>5 4</td>
<td>1.99</td>
<td>2.93</td>
<td>0.45</td>
</tr>
<tr>
<td>Fca77</td>
<td>134</td>
<td>18</td>
<td>2 2</td>
<td>1.01</td>
<td>1.06</td>
<td>0.01</td>
</tr>
<tr>
<td>Fca90</td>
<td>134</td>
<td>18</td>
<td>5 5</td>
<td>2.38</td>
<td>2.78</td>
<td>0.60</td>
</tr>
<tr>
<td>Fca96</td>
<td>134</td>
<td>18</td>
<td>5 3</td>
<td>2.74</td>
<td>2.76</td>
<td>0.63</td>
</tr>
<tr>
<td>Fca132</td>
<td>134</td>
<td>18</td>
<td>5 4</td>
<td>3.02</td>
<td>2.46</td>
<td>0.76</td>
</tr>
<tr>
<td>Fca559</td>
<td>132</td>
<td>18</td>
<td>8 6</td>
<td>3.42</td>
<td>1.81</td>
<td>0.70</td>
</tr>
<tr>
<td>Fca176</td>
<td>130</td>
<td>18</td>
<td>4 6</td>
<td>2.96</td>
<td>2.37</td>
<td>0.72</td>
</tr>
<tr>
<td>Fca35</td>
<td>133</td>
<td>18</td>
<td>2 2</td>
<td>1.92</td>
<td>1.86</td>
<td>0.44</td>
</tr>
<tr>
<td>Lc109</td>
<td>134</td>
<td>18</td>
<td>4 2</td>
<td>2.91</td>
<td>1.53</td>
<td>0.71</td>
</tr>
<tr>
<td>Fca391</td>
<td>133</td>
<td>18</td>
<td>4 3</td>
<td>2.34</td>
<td>2.11</td>
<td>0.53</td>
</tr>
<tr>
<td>Fca08</td>
<td>134</td>
<td>18</td>
<td>2 3</td>
<td>1.74</td>
<td>2.18</td>
<td>0.45</td>
</tr>
<tr>
<td>Fca30</td>
<td>134</td>
<td>18</td>
<td>4 2</td>
<td>1.29</td>
<td>1.25</td>
<td>0.22</td>
</tr>
<tr>
<td>Fca82</td>
<td>121</td>
<td>18</td>
<td>6 3</td>
<td>2.98</td>
<td>2.99</td>
<td>0.61</td>
</tr>
<tr>
<td>Fca149</td>
<td>134</td>
<td>18</td>
<td>3 3</td>
<td>1.41</td>
<td>1.48</td>
<td>0.27</td>
</tr>
<tr>
<td>PcoA208</td>
<td>131</td>
<td>18</td>
<td>3 3</td>
<td>2.59</td>
<td>2.96</td>
<td>0.63</td>
</tr>
<tr>
<td>PcoB10</td>
<td>132</td>
<td>18</td>
<td>7 4</td>
<td>3.23</td>
<td>3.56</td>
<td>0.70</td>
</tr>
<tr>
<td>PcoC112</td>
<td>133</td>
<td>18</td>
<td>4 2</td>
<td>2.57</td>
<td>2.00</td>
<td>0.60</td>
</tr>
<tr>
<td>PcoB210</td>
<td>133</td>
<td>18</td>
<td>5 4</td>
<td>3.58</td>
<td>2.17</td>
<td>0.74</td>
</tr>
<tr>
<td>PcoC108</td>
<td>133</td>
<td>18</td>
<td>3 3</td>
<td>2.86</td>
<td>2.62</td>
<td>0.67</td>
</tr>
</tbody>
</table>

*Effective alleles represent the number of alleles by locus scaled by sample size for cougars in South Dakota and North Dakota.
Table 5.2. Mean and Standard Error of genetic variability metrics for Dakota cougars.

<table>
<thead>
<tr>
<th></th>
<th>South Dakota</th>
<th></th>
<th>North Dakota</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Alleles/Locus</td>
<td>4.3</td>
<td>0.356</td>
<td>3.3</td>
<td>0.282</td>
</tr>
<tr>
<td>Allele with Freq ≥ 5%</td>
<td>3.3</td>
<td>0.252</td>
<td>2.6</td>
<td>0.169</td>
</tr>
<tr>
<td>Effective Alleles/Locus</td>
<td>2.442</td>
<td>0.162</td>
<td>2.223</td>
<td>0.148</td>
</tr>
<tr>
<td># Alleles exclusive to:</td>
<td>1.3</td>
<td>0.291</td>
<td>0.3</td>
<td>0.147</td>
</tr>
<tr>
<td>H&lt;sub&gt;E&lt;/sub&gt;</td>
<td>0.542</td>
<td>0.041</td>
<td>0.504</td>
<td>0.039</td>
</tr>
<tr>
<td>H&lt;sub&gt;O&lt;/sub&gt;</td>
<td>0.547</td>
<td>0.044</td>
<td>0.526</td>
<td>0.046</td>
</tr>
</tbody>
</table>
Table 5.3. Population assignment tests between North Dakota and South Dakota cougars using 20 microsatellite loci.

<table>
<thead>
<tr>
<th>Assigned Population</th>
<th>Sample Pop.</th>
<th>Other Pop.</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Dakota ((n=134))</td>
<td>133</td>
<td>1</td>
</tr>
<tr>
<td>North Dakota ((n=18))</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>149</td>
<td>3</td>
</tr>
<tr>
<td>Percent</td>
<td>98%</td>
<td>2%</td>
</tr>
</tbody>
</table>
Table 5.4. Comparison of observed heterozygosity ($H_O$) levels of cougars in the Black Hills with other cougar populations and other carnivore species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Region</th>
<th>$H_O$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cougar</td>
<td>Black Hills</td>
<td>0.55</td>
<td>(Thompson 2009; 20 loci)</td>
</tr>
<tr>
<td>Cougar</td>
<td>N. Yellowstone</td>
<td>0.56</td>
<td>(Biek et al. 2006; 11 loci)</td>
</tr>
<tr>
<td>Cougar</td>
<td>Utah</td>
<td>0.47</td>
<td>(Sinclair et al. 2001; 9 loci)</td>
</tr>
<tr>
<td>Cougar</td>
<td>Western U.S.</td>
<td>0.42-0.52</td>
<td>(Culver et al. 2000; 10 loci)</td>
</tr>
<tr>
<td>Cheetah*</td>
<td>South Africa</td>
<td>0.39</td>
<td>(Menotti-Raymond and O'Brien 1995)</td>
</tr>
<tr>
<td>African Lion*</td>
<td>Africa</td>
<td>0.66</td>
<td>(Menotti-Raymond and O'Brien 1995)</td>
</tr>
<tr>
<td>Leopard*</td>
<td>Africa</td>
<td>0.77</td>
<td>(Spong et al. 2000)</td>
</tr>
<tr>
<td>Brown Bear*</td>
<td>Kodiak Islands</td>
<td>0.30</td>
<td>(Patkeau et al. 1998)</td>
</tr>
<tr>
<td>Gray Wolf*</td>
<td>U.S.</td>
<td>0.54</td>
<td>(Roy et al. 1994)</td>
</tr>
</tbody>
</table>

*Cheetah (*Acinonyx jubatis*), African lion (*Panthera leo*), leopard (*Panthera pardus*), brown bear, (*Ursus arctos*), and gray wolf (*Canis lupus*).
CHAPTER 6. INDICATORS OF DENSITY DEPENDENCE IN A SEMI-ISOLATED RECOLONIZED COUGAR POPULATION.

Abstract

Since the inception of wildlife conservation and management a common source of debate among professionals has been the concept of population carrying capacity and associated effects of density dependence. Agencies responsible for management of large carnivores have attempted to assess management regimes based on population status of primary prey and suitable habitat. Our objective was to identify and quantify indicators associated with population saturation and density dependence as they relate to cougars (Puma concolor) in the Black Hills of South Dakota and Wyoming. The cougar population in the Black Hills was nearly extirpated by the early to mid 1900s and has recolonized the area via immigration in concert with remnant individuals that likely occupied rugged, isolated habitats of the region. Assessment of this cougar population was initiated in 1985. Intensive research began in 1998; cougars were captured, immobilized, and fitted with radio transmitters. Radioed cougars were monitored weekly from fixed-wing aircraft using aerial telemetry techniques. Animal locations were plotted in ArcGIS; home-range (90% Adaptive Kernel) and dispersal characteristics were calculated. All known mortalities were recorded throughout the Black Hills and carcasses were necropsied to assess diet and quantify body condition. We identified several primary factors indicating density dependence: decrease in female home-range size, increased home-range overlap, increased female dispersal and decreased philopatry,
neonate sex ratios skewed to male kittens, increased mortality related to intraspecific strife, infanticide and emaciation, and a decrease in body condition. A correct assessment of population level is essential to establish appropriate conservation and management scenarios, especially when harvest is an active management technique.

Keywords: cougar, *Puma concolor*, density dependence, carrying capacity, population demographics, Black Hills, South Dakota, Wyoming.

**Introduction**

Since the term carrying capacity as it relates to wildlife conservation and management was first defined by Aldo Leopold (1933) in *Game Management* there has been heated discussion and debate over its meaning. Leopold stated that carrying capacity was “the maximum density of wild game which a particular range is capable of carrying”. Early discussion on the topic generally dealt with ungulate populations and the amount of resources the habitat provided to maintain a number of individuals within said habitat or region (Leopold 1933, Edwards and Fowle 1955). In terms of the functional workings of density dependence, population saturation, and carrying capacity the population in essence regulates itself, ebbing and flowing around a level within the constrains of the habitat and resource availability. When dealing with population management (e.g., harvest management schemes), wildlife populations are usually managed based on objectives related to a carrying capacity level once determined. The issue of habitat and resources regulating wildlife and the actual level and associated number of individuals defined as a population’s carrying capacity is where a great deal of
the debate occurs (Edwards and Fowle 1955, Caugley 1979, Price 1999). An assessment of factors contributing to density dependence in wildlife and quantification of some of these factors is important in order to maintain a scientifically rigorous evaluation of population status.

While carrying capacity and its relation to resource use and dependence have been studied in many ungulate populations (McCullough 1979, McShea et al. 1997, Jordan et al. 2000, Beck et al. 2006), the issue has not been studied as rigorously in large carnivore populations in North America. This omission is quite possibly exacerbated by the fact that many large carnivores were significantly depleted or regionally extirpated during the late 1800s and early 1900s throughout North America. Cougars (*Puma concolor*) were extirpated from eastern North America by the 1900s with the exception of the Florida panther; however, many populations were able to remain extant in rugged terrain throughout the western United States and Canada (Logan and Sweanor 2001, Pierce and Bleich 2003). Although reduced in numbers, populations recolonized and grew significantly when bounties ceased, protection was initiated, and prey species recovered from the era of market hunting.

Cougar populations were generally considered to be increasing throughout their western range towards the end of the twentieth century (CWGMG 2005). Nevertheless, many early management and harvest scenarios were based more on speculation and observations rather than strong science (CWGMG 2005). Within the last twenty years agencies charged with the management of many large carnivores, including cougars, have been accused of using “unsound science” in their management techniques; agencies have
responded to these accusations by increasing knowledge of populations through intensive research, modeling, and adaptive management scenarios aimed at addressing issues of stakeholders involved with charismatic megafauna. Increased technology of tracking equipment, along with use of noninvasive techniques to monitor populations have allowed biologists to gain a better understanding of cryptic carnivores. Despite the intensive knowledge and techniques applied, many populations are managed based on a level of carrying capacity that is at times speculative. Our primary objective was to identify and quantify major indicators of density dependent effects associated with carrying capacity of a free-ranging cougar population. Identifying these factors could help agencies attempting to manage and conserve source and sink cougar populations that may be at differing levels of growth and abundance.

We studied a cougar population located in the Black Hills of western South Dakota and eastern Wyoming to document and quantify factors associated with density dependence and carrying capacity. The newly recolonized cougar population of the Black Hills allows for a unique perspective relative to many extant cougar populations elsewhere. The cougar population of the Black Hills was nearly if not entirely extirpated from the region by the early 1900s (Fecske 2003, Anderson et al. 2004). Although sporadic sightings occurred throughout the 20th century it was not until the mid 1980’s that the South Dakota Department of Game, Fish and Parks (SDGFP) began compiling a list with locations of verified sightings and acknowledged an established, small breeding population within the Black Hills ecosystem. The Black Hills cougar population rebounded naturally (Fecske 2003) with statewide protection adopted in 1978. While the
cougar population was recolonizing the area, primary prey species (white-tailed deer \textit{Odocoileus virginianus}, mule deer \textit{O. hemionus}, and elk \textit{Cervus elaphus}) were increasing along with an absence of other primary predators (i.e., wolves \textit{Canis lupus}, grizzly bears \textit{Ursus arctos}). These intersecific competitors were extirpated similar to the time that cougars were significantly reduced (Higgins et al. 2000). As the cougar population grew in abundance, there was need to scientifically assess the population. Intensive research was initiated in 1998, offering a long-term data set for analysis. The geographical setting of the Black Hills offers a unique perspective in that the region is separated from western breeding populations by more than 100 km of prairie habitat (Fecske 2003), and because it is on the eastern edge of current cougar distribution (with the exception of the Florida panther). Although not considered isolated like the Florida panther, the situation in the Black Hills ecosystem allowed an assessment of a population that has rebounded from near extirpation to become a viable breeding population, and to evaluate changes that have occurred to the population over the past 10 to 20 years.

Study Area

The Black Hills are located in west-central South Dakota and northeastern Wyoming, representing the eastern most extension of the Rocky Mountains, and corresponding in age to the oldest mountains in North America (Froiland 1990). Our study area encompassed the Black Hills, covering approximately 8,400 km$^2$ (Figure 1.1). The Black Hills are a dome-shaped structure, sloping more steeply to the east than from the west with highest elevation of 2,207 m (Froiland 1990). Soils of the Black Hills have been identified as the Gray Wooded soil region, which is unique to South Dakota.
These soils were largely developed under timber in dry sub-humid to humid climate and were derived from limestone, sandstone, and local alluvium from igneous and metamorphic rocks (Froiland 1990). The Black Hills ecosystem is comprised of four distinct vegetation complexes: 1) Rocky Mountain coniferous forest, 2) Northern coniferous forest, 3) Grassland complex, and 4) Deciduous complex. Forest cover in the Black Hills is predominantly ponderosa pine (*Pinus ponderosa*) with codominants of white spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*). The Black Hills are an isolated mountain range, being completely surrounded by the Northern Great Plains.

Primary prey species of cougars on the study area included: white-tailed deer, mule deer, elk, bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*) and porcupine (*Erethizon dorsatum*), along with assorted small mammal species and domestic livestock species. The predator guild of the Black Hills included coyote (*Canis latrans*) and bobcat (*Lynx rufus*); gray wolf, grizzly bear, and black bear (*Ursus americanus*) were been extirpated from the region around the late 1800s to early 1900s (Higgins et al. 2000).

Methods

We captured cougars in 1998 - 2006 throughout the Black Hills study area primarily with the aid of hounds. We were opportunistic in capture techniques; however, we used walk-in live traps, foot-hold snares (Logan et al. 1999), and leg-hold traps with offset jaws opportunistically. We immobilized cougars using a telazol (2.2 mg/lb) and xylazine (0.45 mg/lb) mixture (Kreeger 1996) based on live animal body weight.
Cougars were aged by tooth wear and pelage description (Anderson and Lindzey 2000), and animals > 10 months old were fitted with adult VHF radio-transmitters (Telonics, Inc., Mesa, Arizona, USA). Immobilized cougars were reversed (0.125 mg/kg), released on site, and observed from a distance to assure safe recovery. We captured kittens (< 2 months old) of radio-marked females by hand to determine age of independence and dispersal. Kittens were fitted with expandable VHF radio-collars (Telonics, Inc., Mesa, Arizona, USA). Kittens > 3 months old were fitted with eartag radio-transmitters (Telonics, Inc., Mesa, Arizona, USA), and recaptured when ≥ 10 months old and fitted with adult transmitters (eartag transmitters removed). All captured cougars were eartagged regardless of age or sex.

We located study animals weekly via aerial telemetry from a fixed-wing aircraft, along with ground triangulation and visual observation between flights. The high road density (>13,411 km of inventoried roads within the forest boundary; United States Department of Agriculture Forest Service 2007) of the Black Hills allowed access throughout the majority of the study area for use of ground triangulation. In situations where all littermates were not radio marked, we used visual observation and track counts to increase assessment of kitten survival. We classified animals as: kitten-still dependent on mother, subadult-independent but not part of the breeding population, and adult-animal occupying a resident home-range within the study area. We used Kaplan-Meier Staggered Entry techniques (Pollock et al. 1989) to calculate annual survival between sex and age classes. We used two techniques for assessing mortality. We documented cause-specific mortality of radio-collared animals continuously throughout the project as well
as documenting known cougar mortalities that occurred within the study area. All carcasses were necropsied at South Dakota State University (Brookings, South Dakota, USA) to determine cause of death. We also documented age and sex of carcasses to develop age/sex ratios of known mortalities. Known cougar mortalities were recorded beginning in 1998 in South Dakota allowing trend data related to deaths/year and cause of death. We tabulated types of mortality on an annual basis. We documented total number of reported cougar sightings annually throughout the study area from 1998 - 2006.

All animal locations were entered into ArcGIS (ESRI, Redlands, California, USA). Home-ranges were calculated (95% Adaptive Kernel) using the Home-range Extension in ArcGIS. We chose bandwidths that resulted in the lowest least squares crossed validation scores (LSCV) to create smoothed home-range polygons (J. G. Kie, Idaho State University, pers. comm.). Dispersal distances were calculated from capture point to: site of death, last known location, or home-range center-point if the animal dispersed and successfully established a home-range. In instances where kittens were captured from the den we used the natal home-range center-point versus the site of capture to calculate total dispersal distance. Cougars that established home-ranges with > 5% overlap of natal home-ranges were considered philopatric (Sweanor et al. 2000). If an animal established a home-range within the study area we considered it successfully recruited into the Black Hills cougar population. We calculated home-range overlap (Logan and Sweanor 2001) for cougars with adjacent/overlapping home-ranges.
We initially assessed nutritional condition of animals by classifying heart, kidney, mesentery and subcutaneous fat levels as High, Moderate, or Low by visually observing amount of fatty tissue in the area with consistency of observer. We further quantified kidney fat levels using a technique developed by Riney (1955), allowing an assessment of quantifiable fat levels over time. In essence, a ratio of kidney fat weight to kidney weight was calculated for individual cougars and used as an index to condition. Once nutritional indices were calculated we compared values temporally and used ANOVA to compare kidney fat levels through time.

Results

We captured 35 independent cougars for survival and home-range analyses ($n = 15$ males; $20$ females). We tracked males and females an average of 600.8 days (range: 53 - 2440 days) and 599.5 days (range: 50 - 2081 days), respectively. Annual female survival averaged $0.85$ (SE $0.07$) from 2000 - 2005 (Table 6.1), and annual male survival averaged $0.82$ (SE $0.08$; Table 6.1). We did not note a significant change in cougar survival between years, however low sample size in early years decreased power for statistical analyses. We calculated annual home-ranges for resident females ($n = 32$) and resident males ($n = 20$) between the years 1999-2005 (Table 6.2). Annual home-range size varied for males and females through time. Because of sample size constraints, we separated annual home-ranges into two-year groups (1999 - 2003 and 2004 - 2005) and noted a significant decrease ($P = 0.05$) in female home-range size in the latter compared to earlier years (Table 5.2). Adjacent females had $> 80\%$ home-range overlap in both 2004 and 2005. However, due to a lack of adjacent females collared throughout the
population, we were not able to document total home-range overlap across the Black
Hills cougar ecosystem.

We captured 14 subadult male and 10 subadult female cougars in the Black Hills
from 2003 - 2006. We also captured and marked 18 kittens from seven separate litters.
We documented a skewed male to female sex ratio (5:1) in cougar litters on the study
area. No subadult male cougars were recruited into the Black Hills population; all
subadult males (n = 17) dispersed from the study area or died while dispersing (n =
2). Six subadult females were recruited into the population; however, most females
dispersed from their natal areas (n = 6) with several attempting to establish home-ranges
on the edge of suitable habitat within the study area.

We documented 81 mortality events in the Black Hills between 1998 - 2005. Death
associated with vehicular trauma was the primary mortality source (n = 28),
followed by departmental removal (n = 18), incidental snaring (n = 8), intraspecific strife
(n = 6) from interactions or infanticide, and illegal killing (n = 5) (Figure 6.1). We
documented 8 mortality events due to unknown causes. The number of mortality events
recorded annually increased from 1998 - 2005 (Figure 6.2), along with a significant
increase in the number of animals removed for depredation reasons or due to human
safety risk (Figure 6.3). The number of recorded lion sightings throughout the state of
South Dakota increased from 1998 - 2006 (Figure 6.4), coinciding with the increased
number of mortality events, depredation complaints, and human safety complaints. There
was a high correlation between annual mortality events and recorded cougar sightings ($r^2$
= 0.96). The average age of death for cougars in South Dakota was 2.63 years and was
similar \((P>0.50)\) for males and females. A higher number of male mortalities \((n = 45)\) were documented compared to females \((n = 32)\). Of the 77 known mortality events, 12 were considered natural mortality \((15.6 \%)\), with the remaining events \((n = 65; 84.4 \%)\) considered human-induced or human-related causes of mortality. We also documented prevalence of resident male facial scarring. Of 11 resident male cougars captured, 89\% showed moderate to severe scarring primarily across the face and skull along with scarring of the forelimbs (Figure 6.5).

We conducted 84 necropsies \((n = 32 \text{ females}; \ n = 27 \text{ males})\) of cougar carcasses. We documented several \((n = 8)\) emaciated cougars to the point of starvation from 2004 - 2006 (Figure 6.3). Total kidney fat levels of necropsied cougars decreased, for both subadult and adult cougars \((P = 0.07)\). From (1998 – 2003) subadult \((n = 14)\) and adult \((n = 11)\) cougar kidney fat indices averaged 167.6 (SE 17.7), and 161.2 SE (20.0) respectively. For the latter time period (2004 – 2005) mean kidney fat levels decreased for both subadults \((n = 23, \text{ mean } = 118.54 \text{ SE } 13.8)\) and adults \((n = 12, \text{ mean } = 144.18 \text{ SE } 19.2)\). We found no differences in kidney fat indices with age*year comparisons \((P = 0.37)\) or when comparing age \((P = 0.59)\).

**Discussion**

Cougars have been documented with high home-range overlap and densities in California cougar populations (Pierce et al. 2000). The Black Hills cougar population shares the aspects of these characteristics with cougar populations considered to be indicating intrapopulation density dependent effects. Probably the more striking examples of population saturation in Black Hills cougars are decreased female home-
ranges coupled with >80% home-range overlap, and a decrease in body condition (based on kidney fat levels) with increased instances of emaciation. Although a significant decline in home-range size of males was not found we did document a high level of intraspecific fighting among male cougars while defending territories. Other research has noted facial scarring (Logan and Sweanor 2001); however, limited scarring occurred on males when we began studying this population in the late 1990’s (D. Fecske, ND Game and Fish, person. commun.). Sargent and Ruff (1999) suggested populations must indicate reduced reproduction and growth rates in order to document carrying capacity. Although we did not see a decrease in reproductive rates per se; increased mortality, dispersal, and changes related to land tenure suggested the population was at a level where density dependence was affecting the population’s life history as a whole.

We did not document a significant change in survival rates despite an almost exponential increase in mortality events from 1999-2005. According to the Julliard (2000) hypothesis, in higher quality habitats parents should produce more of the most philopatric sex, while in poor environments parents should produce more littermates of the sex that is more prone to disperse from the natal area. Though the habitat in the Black Hills may not be considered “poor” due to competition for resources between philopatric animals, it would be beneficial for females to produce more males which have > 90% dispersal from the study area and therefore would not be in direct competition with their mother or siblings. We documented a highly skewed male sex ratio in cougar litters (5:1), and suggest the male skewed birth ratio of Black Hills cougars produces an effect similar to
decreasing the overall reproductive output. A higher proportion of subadult females dispersing from natal area (60%) also may be indicative of resource competition.

The use of sightings data regarding population status has been criticized (CWGMG 2005). We believe that the trend data can be useful if coupled with empirical data from the population. A near exponential increase in cougar sightings as was found in South Dakota corresponded to increased number of cougars documented through research. There sometimes seems to be a “hysteria” component within the human complex associated with newly developing or recolonizing carnivore populations, which could result in an increase in reported sightings. This effect may be evaluated by comparing sighting trend data with field data and establishing if a true correlation exists, rather than inflated sightings due to subliminally influenced interest. The high correlation between mortality events and sighting data noted in the Black Hills, suggests reliable recording of sighting data may an important parameter to be used as another tool in the spectrum to assess cougar populations especially in areas where cougars are recolonizing. It would also be beneficial to assess stakeholder acceptance of cougars while documenting cougar sightings.

An essential aspect affecting the cougar population in the Black Hills ecosystem is an overall lack of competition from indigenous large carnivores previously extirpated from the region. Wolves and grizzly bears were native to the Black Hills ecoregion and would have competed with cougars for resources, possibly affecting prey availability and cougar movements. Competition between wolves and cougars has been documented in the Yellowstone ecosystem (Smith et al. 2003, Ruth et al. 2004, Kortello et al. 2007),
with cougars generally showing subordination to wolves along with documented cougar mortality from wolves and usurpation of cougar kill sites by wolves (Kortello et al. 2007). Bears displaced cougars from kill sites in Glacier National Park and if recurrent, the authors suggested displacement could affect cougar energy requirements (Murphy et al. 1998). The fact that these top-level carnivores are absent would allow cougars in the Black Hills region to most likely reach population levels and densities higher than were found prior to human colonization of the region. We believe that lack of competition from extirpated apex predators allowed cougars to occupy the Black Hills at a density that would be more self-limiting due to density dependence rather than due to interspecific competition for resources.

Possibly most important in the discussion of cougar carrying capacity is that there is not necessarily one clear indicator of density dependence. A holistic-minded approach, assessing population demographic variables that may be indicative of competition for resources is needed to accurately state whether the population appears to be at a stable level, increasing, or declining. Snapshots in time may be difficult to use in order to assess the population level, however when combined with data, such as survival/mortality, recruitment, sightings, long-term data sets, and harvest age/sex data, management agencies should be able to better assess cougar population status.

Management Implications

When using harvest techniques, many state agencies manage game species based on a maximum sustained yield, which is based on population carrying capacity. Documenting factors associated with a population at a level of carrying capacity is
important. We identified several factors that indicated the Black Hills cougar population was at a level that would be considered at or above carrying capacity for the region. Factors associated with density dependent effects identified in our study population would be applicable to other cougar populations and could be used to assess population status as it relates to carrying capacity and management objectives. We add that direct comparison of certain values, such as home-range size and density between separate populations may lead to erroneous conclusions because on the differential techniques involved to calculate these values. The ruggedness of the terrain and habitat quality can greatly affect home-range size, which is why we believe an intrapopulation comparison of home-range values and density through time are more applicable to determine population status versus comparing values between geographically separated populations.

Based on our findings, recording trend data such as cougar sightings and cumulative mortality are important factors for assessing populations. Their importance is also heightened by the ease with which these types of data can be recorded and analyzed. We must add the caveat that without empirical demographic data for comparison these factors may lead to higher levels of speculation as it relates to overall population size. Although the use of sighting data has been criticized if used as an index for assessing population status, the high correlation between mortality and sightings data, coupled with our field data from the Black Hills suggest that the increase in sightings was concurrent with an increase in the cougar population throughout the Black Hills. While we do not consider sighting data a reliable technique in itself, the relevance of using data from
sightings may be especially important in regions that are experiencing expansion and resurgence of cougars.

Aside from the obvious sex and age characteristics obtained from mandatorily checked animals during harvest and their importance in assessing harvest effects and population structure (Anderson and Lindzey 2005), agencies could assess body condition based on fat levels. With many states using zones/units for harvest regimes, the possibility of comparing body condition between management zones and ecoregions within the management area based on fat level indices could add further insight into source/sink population dynamics of a region and allow for more landscape level analyses.

Across the range of cougars throughout most of North America, the primary interspecific predatorial competition (e.g., grizzly bears and wolves) has been extirpated or severely reduced. This lack of competition may be a key factor in the resurgence of cougar populations in many regions during the past 20 years. Along those lines, the Black Hills has seen a dramatic increase in elk and white-tailed deer throughout the 20th Century (Froiland 1990, Huxoll 2006), in addition to the introduction of bighorn sheep, mountain goats, and wild turkeys (Meleagris gallopavo), which are all documented cougar prey species (Pierce and Bleich 2003). Based on our findings, coupled with increased prey, decreased interspecific competition, and in conjunction with the literature related to cougar expansion, we postulate that cougars in the Black Hills may currently occur at higher numbers than they were prior to European settlement of the area.
Literature Cited


http://www.easterncougarnet.org/.


Froiland, S. G. 1990. Natural History of the Black Hills and Badlands. The Center for Western Studies, Augustana College, Sioux Falls, South Dakota USA.


Leopold, A. S. 1933. Game Management. Scribners, New York, USA.


Table 6.1. Annual survival rate estimates ($S_i$) for independent aged cougars in the Black Hills of South Dakota, 1999 - 2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males (N)</th>
<th>Annual Male $S_i$</th>
<th>Females (N)</th>
<th>Annual Female $S_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>4</td>
<td>0.75</td>
<td>0</td>
<td>N/A</td>
</tr>
<tr>
<td>2000</td>
<td>3</td>
<td>0.67</td>
<td>4</td>
<td>0.75</td>
</tr>
<tr>
<td>2001</td>
<td>2</td>
<td>1.00</td>
<td>3</td>
<td>1.00</td>
</tr>
<tr>
<td>2002</td>
<td>3</td>
<td>1.00</td>
<td>4</td>
<td>0.50</td>
</tr>
<tr>
<td>2003</td>
<td>7</td>
<td>1.00</td>
<td>5</td>
<td>1.00</td>
</tr>
<tr>
<td>2004</td>
<td>8</td>
<td>0.50</td>
<td>13</td>
<td>0.92</td>
</tr>
<tr>
<td>2005</td>
<td>5</td>
<td>0.80</td>
<td>16</td>
<td>0.94</td>
</tr>
</tbody>
</table>

Mean = 4.57 0.82 (SE 0.07) 7.5 0.85 (SE 0.08)
Table 6.2. Annual home-range (HR) values (Mean ± 1SE) for adult cougars in the Black Hills of South Dakota and Wyoming, 1999 - 2005.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males (N)</th>
<th>Annual HR (km²)</th>
<th>Females (N)</th>
<th>Annual HR (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>4</td>
<td>466.3 ± 134.0</td>
<td>0</td>
<td>N/A</td>
</tr>
<tr>
<td>2000</td>
<td>3</td>
<td>936.4 ± 154.2</td>
<td>2</td>
<td>457.1 ± 60.4</td>
</tr>
<tr>
<td>2001</td>
<td>3</td>
<td>968.8 ± 183.6</td>
<td>4</td>
<td>304.6 ± 62.6</td>
</tr>
<tr>
<td>2003</td>
<td>4</td>
<td>684.7 ± 152.4</td>
<td>3</td>
<td>147.6 ± 49.1</td>
</tr>
<tr>
<td>2004</td>
<td>4</td>
<td>397.3 ± 54.4</td>
<td>5</td>
<td>105.2 ± 27.3</td>
</tr>
<tr>
<td>2005</td>
<td>2</td>
<td>457.1 ± 60.4</td>
<td>9</td>
<td>123.4 ± 32.9</td>
</tr>
</tbody>
</table>

Mean = 3.3  641.1 ± 70.9  4.6  139.6 ± 18.3
Figure 6.1. Breakdown (%) of mortality events \((n = 85)\) documented for cougars in South Dakota 1998 - 2005.
Figure 6.2. Annual cougar mortality events documented in South Dakota, 1998 - 2005.
Figure 6.3. Annual mortality events attributed to removal of nuisance animals (depredation and human safety risk), and emaciation/starvation in the Black Hills, 2000 - 2006.
Figure 6.4. Annual number of cougar reports/sightings documented in South Dakota, 1996 - 2006.
Figure 6.5. Examples of facial scarring of adult male cougars due to intraspecific encounters in the Black Hills of South Dakota, 2004 - 2006.
Appendix A. Body measurements, sex, and age characteristics of cougars captured in the Black Hills, 2003 - 2006. (FPL – Front foot plantar pad length, FPW – Front foot plantar pad width, HPL – Hind foot plantar pad length, HPW – Hind foot plantar pad width.)

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Sex</th>
<th>Age (yrs)</th>
<th>Weight (kg)</th>
<th>Total Length (cm)</th>
<th>Tail Length (cm)</th>
<th>Neck Girth (cm)</th>
<th>Chest Girth (cm)</th>
<th>FPL (mm)</th>
<th>FPW (mm)</th>
<th>HPL (mm)</th>
<th>HPW (mm)</th>
<th>Upper Canines (mm)</th>
<th>Lower Canines (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F21</td>
<td>F</td>
<td>1.5</td>
<td>88</td>
<td>195</td>
<td>71</td>
<td>35</td>
<td>66</td>
<td>36</td>
<td>53</td>
<td>34</td>
<td>47</td>
<td>23</td>
<td>18</td>
</tr>
<tr>
<td>F22</td>
<td>F</td>
<td>1.5</td>
<td>85</td>
<td>197</td>
<td>77</td>
<td>34.5</td>
<td>60</td>
<td>38</td>
<td>50</td>
<td>40</td>
<td>50</td>
<td>24</td>
<td>15</td>
</tr>
<tr>
<td>F23</td>
<td>F</td>
<td>1.5</td>
<td>90</td>
<td>197</td>
<td>75</td>
<td>43</td>
<td>70</td>
<td>39</td>
<td>54</td>
<td>36</td>
<td>49</td>
<td>23</td>
<td>18</td>
</tr>
<tr>
<td>F24</td>
<td>F</td>
<td>1.5</td>
<td>72</td>
<td>183</td>
<td>74.5</td>
<td>31</td>
<td>63</td>
<td>36</td>
<td>50</td>
<td>35</td>
<td>45</td>
<td>21</td>
<td>20</td>
</tr>
<tr>
<td>F25</td>
<td>F</td>
<td>3</td>
<td>102</td>
<td>197</td>
<td>70</td>
<td>37</td>
<td>68.5</td>
<td>38</td>
<td>54</td>
<td>35</td>
<td>44</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td>F26</td>
<td>F</td>
<td>4.5</td>
<td>104</td>
<td>191</td>
<td>73</td>
<td>39</td>
<td>70</td>
<td>47</td>
<td>60</td>
<td>44</td>
<td>50</td>
<td>24</td>
<td>19.5</td>
</tr>
<tr>
<td>F27</td>
<td>F</td>
<td>3.5</td>
<td>82</td>
<td>202</td>
<td>77</td>
<td>35</td>
<td>62</td>
<td>48</td>
<td>38</td>
<td>46</td>
<td>34</td>
<td>26</td>
<td>15</td>
</tr>
<tr>
<td>F28</td>
<td>F</td>
<td>1.5</td>
<td>82</td>
<td>200</td>
<td>82</td>
<td>33</td>
<td>66</td>
<td>41</td>
<td>45</td>
<td>37</td>
<td>49</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>M30</td>
<td>M</td>
<td>0.5</td>
<td>48</td>
<td>97</td>
<td>59</td>
<td>31</td>
<td>55</td>
<td>37</td>
<td>51</td>
<td>35</td>
<td>47</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>F9</td>
<td>F</td>
<td>8.50</td>
<td>99</td>
<td>209</td>
<td>81</td>
<td>39</td>
<td>70</td>
<td>40</td>
<td>40</td>
<td>38</td>
<td>51</td>
<td>22.5</td>
<td>20</td>
</tr>
<tr>
<td>F18</td>
<td>F</td>
<td>4.5</td>
<td>120</td>
<td>198</td>
<td>78</td>
<td>36</td>
<td>70</td>
<td>39</td>
<td>55</td>
<td>37</td>
<td>45</td>
<td>21</td>
<td>20</td>
</tr>
<tr>
<td>M12</td>
<td>M</td>
<td>5</td>
<td>158</td>
<td>213</td>
<td>85</td>
<td>42</td>
<td>82</td>
<td>45</td>
<td>65</td>
<td>46</td>
<td>62</td>
<td>30.5</td>
<td>24</td>
</tr>
<tr>
<td>M31</td>
<td>M</td>
<td>1.5</td>
<td>90</td>
<td>213</td>
<td>81</td>
<td>37</td>
<td>64.5</td>
<td>39</td>
<td>55</td>
<td>39</td>
<td>51</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>M32</td>
<td>M</td>
<td>1.5</td>
<td>92</td>
<td>211</td>
<td>83</td>
<td>38.5</td>
<td>69.5</td>
<td>42</td>
<td>60</td>
<td>39</td>
<td>52</td>
<td>27</td>
<td>23</td>
</tr>
<tr>
<td>M36</td>
<td>M</td>
<td>0.58</td>
<td>50</td>
<td>173</td>
<td>69</td>
<td>30</td>
<td>58</td>
<td>32</td>
<td>54</td>
<td>32</td>
<td>44</td>
<td>18.5</td>
<td>18</td>
</tr>
<tr>
<td>M41</td>
<td>M</td>
<td>1</td>
<td>102</td>
<td>199</td>
<td>69</td>
<td>35.5</td>
<td>67</td>
<td>40</td>
<td>63</td>
<td>40</td>
<td>55</td>
<td>29</td>
<td>23</td>
</tr>
<tr>
<td>M44</td>
<td>M</td>
<td>1.5</td>
<td>100</td>
<td>216</td>
<td>85</td>
<td>34</td>
<td>66</td>
<td>39</td>
<td>59</td>
<td>36</td>
<td>55</td>
<td>24</td>
<td>21</td>
</tr>
<tr>
<td>F46</td>
<td>F</td>
<td>1.75</td>
<td>93</td>
<td>208</td>
<td>80</td>
<td>35</td>
<td>66</td>
<td>37</td>
<td>56</td>
<td>34</td>
<td>49</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>F47</td>
<td>F</td>
<td>2</td>
<td>100</td>
<td>211</td>
<td>84</td>
<td>34</td>
<td>67</td>
<td>40</td>
<td>54</td>
<td>39</td>
<td>51</td>
<td>25</td>
<td>22</td>
</tr>
<tr>
<td>Animal ID</td>
<td>Sex</td>
<td>Age (yrs)</td>
<td>Weight (kg)</td>
<td>Total Length (cm)</td>
<td>Tail Length (cm)</td>
<td>Neck Girth (cm)</td>
<td>Chest Girth (cm)</td>
<td>FPL (mm)</td>
<td>FPW (mm)</td>
<td>HPL (mm)</td>
<td>HPW (mm)</td>
<td>Upper Canines (mm)</td>
<td>Lower Canines (mm)</td>
</tr>
<tr>
<td>-----------</td>
<td>-----</td>
<td>----------</td>
<td>-------------</td>
<td>------------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>----------</td>
<td>---------</td>
<td>----------</td>
<td>-------</td>
<td>-------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>F23</td>
<td>F</td>
<td>3</td>
<td>100</td>
<td>191</td>
<td>66</td>
<td>37</td>
<td>71</td>
<td>45</td>
<td>55</td>
<td>42</td>
<td>50</td>
<td>25</td>
<td>20</td>
</tr>
<tr>
<td>F22</td>
<td>F</td>
<td>2.5</td>
<td>99</td>
<td>200</td>
<td>79</td>
<td>32</td>
<td>65</td>
<td>40</td>
<td>55</td>
<td>36</td>
<td>49</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>F49</td>
<td>F</td>
<td>0.46</td>
<td>45</td>
<td>156</td>
<td>54</td>
<td>28</td>
<td>54</td>
<td>43</td>
<td>55</td>
<td>36</td>
<td>45</td>
<td>10</td>
<td>8.5</td>
</tr>
<tr>
<td>M50</td>
<td>M</td>
<td>8</td>
<td>156</td>
<td>222</td>
<td>91</td>
<td>41</td>
<td>72.5</td>
<td>47</td>
<td>68</td>
<td>42</td>
<td>52</td>
<td>30.5</td>
<td>22</td>
</tr>
<tr>
<td>F55</td>
<td>F</td>
<td>5.5</td>
<td>95</td>
<td>214</td>
<td>84</td>
<td>35</td>
<td>64.5</td>
<td>40</td>
<td>56</td>
<td>36</td>
<td>49</td>
<td>26</td>
<td>20</td>
</tr>
<tr>
<td>F56</td>
<td>F</td>
<td>1.5</td>
<td>85</td>
<td>200</td>
<td>80</td>
<td>34</td>
<td>67</td>
<td>36</td>
<td>53</td>
<td>32</td>
<td>49</td>
<td>22</td>
<td>17</td>
</tr>
<tr>
<td>M57</td>
<td>M</td>
<td>9</td>
<td>162</td>
<td>222</td>
<td>78</td>
<td>44</td>
<td>76</td>
<td>50</td>
<td>70</td>
<td>45</td>
<td>58</td>
<td>31</td>
<td>24</td>
</tr>
<tr>
<td>M58</td>
<td>M</td>
<td>4.5</td>
<td>148</td>
<td>216</td>
<td>80</td>
<td>39</td>
<td>73</td>
<td>44</td>
<td>64</td>
<td>43</td>
<td>50</td>
<td>27.5</td>
<td>23</td>
</tr>
<tr>
<td>F9</td>
<td>F</td>
<td>-</td>
<td>79</td>
<td>199</td>
<td>74</td>
<td>33</td>
<td>62.5</td>
<td>39</td>
<td>61</td>
<td>37</td>
<td>52</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td>F60</td>
<td>F</td>
<td>3.5</td>
<td>80</td>
<td>196</td>
<td>79</td>
<td>36</td>
<td>65</td>
<td>37</td>
<td>57</td>
<td>37</td>
<td>46</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>F61</td>
<td>F</td>
<td>4.5</td>
<td>108</td>
<td>196</td>
<td>75</td>
<td>33.5</td>
<td>65</td>
<td>35</td>
<td>54</td>
<td>35</td>
<td>46</td>
<td>25</td>
<td>20.5</td>
</tr>
<tr>
<td>F45</td>
<td>F</td>
<td>1</td>
<td>60</td>
<td>189</td>
<td>76</td>
<td>29</td>
<td>50</td>
<td>36</td>
<td>52</td>
<td>32</td>
<td>44</td>
<td>22</td>
<td>18</td>
</tr>
<tr>
<td>F62</td>
<td>F</td>
<td>2</td>
<td>80</td>
<td>196</td>
<td>76</td>
<td>31</td>
<td>61</td>
<td>33</td>
<td>54</td>
<td>34</td>
<td>44</td>
<td>21</td>
<td>19</td>
</tr>
<tr>
<td>M1</td>
<td>M</td>
<td>11</td>
<td>175</td>
<td>221</td>
<td>77</td>
<td>38</td>
<td>79</td>
<td>50</td>
<td>65</td>
<td>41</td>
<td>58</td>
<td>14.5</td>
<td>23.5</td>
</tr>
<tr>
<td>M4</td>
<td>M</td>
<td>8</td>
<td>159</td>
<td>201</td>
<td>81</td>
<td>42.5</td>
<td>81</td>
<td>45</td>
<td>69</td>
<td>41</td>
<td>59</td>
<td>29.5</td>
<td>23</td>
</tr>
<tr>
<td>F65</td>
<td>F</td>
<td>4.5</td>
<td>82</td>
<td>198</td>
<td>77</td>
<td>32.5</td>
<td>60</td>
<td>35</td>
<td>53</td>
<td>29</td>
<td>45</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>M66</td>
<td>M</td>
<td>6.5</td>
<td>150</td>
<td>215</td>
<td>88</td>
<td>43</td>
<td>79.5</td>
<td>43</td>
<td>66</td>
<td>43</td>
<td>50</td>
<td>27.5</td>
<td>23</td>
</tr>
<tr>
<td>F67</td>
<td>F</td>
<td>2</td>
<td>101</td>
<td>207</td>
<td>82</td>
<td>35</td>
<td>64</td>
<td>37</td>
<td>52</td>
<td>36</td>
<td>51</td>
<td>22</td>
<td>20</td>
</tr>
<tr>
<td>F68</td>
<td>F</td>
<td>1.5</td>
<td>80</td>
<td>195</td>
<td>72</td>
<td>33</td>
<td>60</td>
<td>36</td>
<td>55</td>
<td>35</td>
<td>48</td>
<td>22</td>
<td>18</td>
</tr>
<tr>
<td>M69</td>
<td>M</td>
<td>0.46</td>
<td>48</td>
<td>162</td>
<td>65</td>
<td>26</td>
<td>57.5</td>
<td>32</td>
<td>47</td>
<td>32</td>
<td>40</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td>F70</td>
<td>F</td>
<td>1.5</td>
<td>91</td>
<td>194</td>
<td>72</td>
<td>33</td>
<td>64</td>
<td>33</td>
<td>53</td>
<td>33</td>
<td>48</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>M71</td>
<td>M</td>
<td>2.5</td>
<td>96</td>
<td>208</td>
<td>88</td>
<td>34</td>
<td>61</td>
<td>38</td>
<td>55</td>
<td>36</td>
<td>47</td>
<td>26</td>
<td>22</td>
</tr>
<tr>
<td>M72</td>
<td>M</td>
<td>1.5</td>
<td>100</td>
<td>214.5</td>
<td>85.5</td>
<td>37</td>
<td>68.5</td>
<td>46</td>
<td>59</td>
<td>39</td>
<td>50</td>
<td>27</td>
<td>24</td>
</tr>
<tr>
<td>M73</td>
<td>M</td>
<td>7</td>
<td>174</td>
<td>216</td>
<td>82</td>
<td>40</td>
<td>76.5</td>
<td>46</td>
<td>64</td>
<td>44</td>
<td>52</td>
<td>31.5</td>
<td>24</td>
</tr>
<tr>
<td>F75</td>
<td>F</td>
<td>4</td>
<td>99</td>
<td>211</td>
<td>84</td>
<td>35</td>
<td>62.5</td>
<td>36</td>
<td>53</td>
<td>36</td>
<td>45</td>
<td>23.5</td>
<td>19</td>
</tr>
<tr>
<td>F76</td>
<td>F</td>
<td>5.5</td>
<td>106</td>
<td>211</td>
<td>81</td>
<td>35.5</td>
<td>63</td>
<td>35</td>
<td>51</td>
<td>35</td>
<td>43</td>
<td>25</td>
<td>20</td>
</tr>
<tr>
<td>Animal ID</td>
<td>Sex</td>
<td>Age (yrs)</td>
<td>Weight (kg)</td>
<td>Total Length (cm)</td>
<td>Tail Length (cm)</td>
<td>Neck Girth (cm)</td>
<td>Chest Girth (cm)</td>
<td>FPL (mm)</td>
<td>FPW (mm)</td>
<td>HPL (mm)</td>
<td>HPW (mm)</td>
<td>Upper Canines (mm)</td>
<td>Lower Canines (mm)</td>
</tr>
<tr>
<td>-----------</td>
<td>-----</td>
<td>-----------</td>
<td>-------------</td>
<td>-------------------</td>
<td>------------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>----------</td>
<td>----------</td>
<td>----------</td>
<td>----------</td>
<td>-------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>M78</td>
<td>M</td>
<td>0.92</td>
<td>62</td>
<td>178</td>
<td>72</td>
<td>30</td>
<td>59</td>
<td>38</td>
<td>55</td>
<td>35</td>
<td>48</td>
<td>19.5</td>
<td>15</td>
</tr>
<tr>
<td>M81</td>
<td>M</td>
<td>0.92</td>
<td>59</td>
<td>183</td>
<td>72</td>
<td>27</td>
<td>51.5</td>
<td>36</td>
<td>55</td>
<td>35</td>
<td>45</td>
<td>20</td>
<td>17</td>
</tr>
<tr>
<td>M82</td>
<td>M</td>
<td>4.5</td>
<td>135</td>
<td>221</td>
<td>87</td>
<td>40</td>
<td>73</td>
<td>42</td>
<td>60</td>
<td>44</td>
<td>53</td>
<td>26</td>
<td>22</td>
</tr>
<tr>
<td>F83</td>
<td>F</td>
<td>4.5</td>
<td>81</td>
<td>204</td>
<td>82</td>
<td>34.5</td>
<td>59</td>
<td>36</td>
<td>52</td>
<td>32</td>
<td>46</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>M84</td>
<td>M</td>
<td>6.5</td>
<td>160</td>
<td>223</td>
<td>82</td>
<td>47</td>
<td>80</td>
<td>45</td>
<td>62</td>
<td>43</td>
<td>50</td>
<td>32</td>
<td>25</td>
</tr>
</tbody>
</table>