

ANTHROPOGENIC FACTORS AFFECTING MOUNTAIN LIONS IN THE BLACK
HILLS OF SOUTH DAKOTA

BY

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Doctor of Philosophy

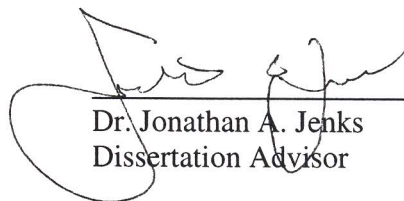
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This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply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


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Abstract

Anthropogenic Factors Affecting Mountain Lions in the Black Hills of South Dakota

Brian D. Jansen

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Historically, mountain lions (*Puma concolor*) in North America were persecuted, at least since European colonization. The distribution of mountain lions declined for decades until in the mid-1900s, when they persisted only in the mountains of western North America and wetlands of the Florida peninsula. After legal protection and human regulation of mortality in the 1970s, mountain lion distribution increased, which is evident by the return of breeding populations in both, North and South Dakota, as well as increased sightings in Nebraska. Mountain lions interact with humans throughout their distribution but many aspects of the mountain lion/human interface remains unknown. The Black Hills of South Dakota are dominated by human activity; from residences interspersed in mountain lion habitat to the recreational opportunities that involve the species. Based on the distribution of humans and mountain lions in the Black Hills ecosystem, there is scarcely a mountain lion home area that does not contain at least 1 human residence; because of the presence of humans, mountain lions are forced to interact with people in some way. In 1998, the first mountain lion was captured in South Dakota for scientific research. Intensive research with numerous individual mountain lions began in 2002. In 2005, South Dakota Department of Game, Fish, and Parks,

deemed it prudent to permit sport-hunting of mountain lions and because scientific research had been occurring, the opportunity to investigate the relationship between mountain lions and sport-hunting arose. The objectives of this research project were to investigate the relationship between mountain lions and humans in the Black Hills, South Dakota. To this end, we (1) investigated the impact of sport-hunting on mountain lion population demographics, and (2) investigated whether subadult males were more prone to conflict with humans or if they were simply more prevalent in the population, and (3) investigated the relationship between density of human residences and mountain lion survival and disease exposure. We found that sport-hunting of mountain lions negatively impacted cub survival, subadult survival, adult survival, and subadult emigration. Survival of cubs, subadults, and adults was higher in Custer State Park/Wind Cave National Park, where mountain lions were legally protected, than in areas where both sport-hunting and government removal of mountain lions occurred. Subadult dispersal from the study area was high and rates were similar regardless of protected status, although population emigration was higher for animals subjected to hunting, in time and space. We found no changes in litter size or population size in the study area between study periods, suggesting that the population remained stable following the onset of sport-hunting. Human-caused mortality accounted for 65% of deaths of radiocollared animals from 2005 to 2009, with sport-hunting being the largest source of mortality (30%). Department removal, intraspecific strife, and diseases each accounted for 16% of total mortality of radiocollared animals, 2005–2009. We found no evidence that compensation occurred with an increase in sport-hunting and decrease in other forms of

human-caused or natural-caused mortality. Regarding sport-hunting, the mountain lion population remained numerically stable during the first 4 years of sport-hunting; however, survival rates of all age classes declined with increase in harvest quota, especially for adult males. Adult male survival might be an important characteristic here because of the relatively isolated nature of this population and the density-independent and nearly obligate-dispersal of males born in the Black Hills. Adult male numbers are apparently maintained through immigration from other areas with the rate of immigration unknown, suggesting that prudence in human killing of adult males would be in the interest of mountain lion conservation in the Black Hills. Mountain lion-human conflicts occur in the Black Hills, as elsewhere. We found that subadult males were more frequently involved in conflicts of all types than other sex and age classes within the population. Both subadult and adult males were predominantly involved in livestock conflicts, however an important distinction was that livestock conflicts occurred with “hobby” livestock (e.g., Llamas, miniature donkeys), rather than domestic cattle or sheep so prevalent in livestock-lion conflicts in western states. Subadult male and female mountain lions were normally involved in public safety and domestic pet incidents. Adult female mountain lions consistently occurred less frequently in conflicts than they occurred in the population. We hypothesize that intrinsic exploratory behavior and developing hunting skills interact to increase the probability of subadult lions, especially males, coming into conflict with humans over that of adults. Mountain lions in the Black Hills have been exposed to similar diseases at similar rates to other mountain lion populations. We found high rates of exposure to *Mycoplasma haemominutum*,

Toxoplasma gondii, and Feline/Canine Parvovirus. Feline/Canine Parvovirus is an endemic organism that causes digestive tract disease that causes illness in adults, but is often fatal in young animals. Influence of diseases on the population dynamics of mountain lions is unknown in the Black Hills. Although 16% of subadult and adult and 10% of cub mortalities were potentially caused by disease, those rates were low compared to direct mortalities due to humans and intra-specific strife. The ubiquitous distribution of humans in exurban-type development in the Black Hills differs from much of mountain lion habitat in western North America. We found only 3 mountain lions (4%) that resided in areas that did not contain human residences. Adult mountain lion survival declined with increasing proportion of home areas ≤ 200 m from a residence. Mountain lion survival declined below 0.80 when 40% and 60% of the home area was ≤ 200 m from a residence for adult males and females, respectively. We found no evidence of an inverse relationship between disease exposure and the proportion of home areas ≤ 200 m from a residence. Our results indicate that mountain lions can survive within close proximity to human houses given appropriate tolerance. We suggest that regional beliefs and cultural backgrounds support the necessary tolerance for mountain lions and those values would determine the survival curve of mountain lions. Our results could be used as a starting point for landscape planners, but caution is appropriate because of the potential influence of regional values. Future research might gather more data on animals not exposed to houses and animals incorporating higher density of housing into their home areas and with differing regional values from those of western

South Dakota. Public attitudes are important and should be further evaluated in more locales within the distribution of the mountain lion.

These research results are pertinent to the growing body of knowledge of the relationship between mountain lions and humans. The relationship between mountain lions and humans is not only critical to the conservation of mountain lions, but also for meeting conservation objectives for other species that might be influenced by mountain lions, including domestic species that hold significant economic and social value. Our results could be used by wildlife managers to understand the impacts of management decisions on mountain lions. They also could be used by various government agencies when planning future development of areas to support wildlife conservation.

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CHAPTER 1: SPORT-HUNTING AND MOUNTAIN LION POPULATION

DEMOGRAPHICS

Abstract

Sport-hunting mountain lions (*Puma concolor*) in North America is common and the primary method used by government agencies for manipulating populations. Efficacy of sport-hunting to achieve management objectives has not been supported by scientific research and is often challenged. We studied population-level changes in demographic rates before and after the legalization and onset of sport-hunting in the Black Hills, South Dakota. We simultaneously studied mountain lions within and outside of protected areas between 2005 and 2009, after onset of sport-hunting. We used radiocollared mountain lions to track reproductive, survival, and movement characteristics of cubs (<1 yr), subadults (1–3 yrs), and adults (>3 yrs). We captured and followed 275 mountain lions of all sexes and ages between 2002 and 2009. We found no differences in litter sizes between study periods or protected status. Litter sizes ranged from 2.9 to 3.0 cubs/litter in legally hunted and non-hunted areas, respectively. Cub survival through 1 year of age was similar ($\Delta S < 0.02$) between study periods, but was 47% lower in hunted versus protected areas 2005–2009. Subadult survival until dispersal or emigration was lower ($\Delta S_{male} = 0.08$, $\Delta S_{female} = 0.07$) in hunted versus non-hunted periods and areas. Subadult male dispersal from the study area was consistently high (> 88%) regardless of period or areas. Subadult female dispersal was 45% lower in protected areas, than for conspecifics in hunted areas. However, emigration of either sex from the ecological population was higher for those animals born in hunted periods and areas, than for conspecifics not

subjected to hunting. Annual adult survival for either sex declined according to hunting status. Those animals studied during non-hunted periods or within protected areas exhibited higher annual survival than conspecifics subjected to hunting. Causes of mortality were dominated by humans (65–90% human-caused) in both study periods. Government removals and poaching/incidental trapping were the dominant sources of mortality during the non-hunting period, whereas legal hunting was the dominant source of mortality for radiocollared animals during the hunting period. We found no evidence that sport-hunting mortality compensated for lethal-removal by state, motor vehicle collisions, or other human-caused mortality (e.g., poaching, justified shooting, incidental public trapping). We found population size remained numerically and compositionally stable from 2005 to 2009. Although, the Black Hills are isolated by >90 km of open prairie, mortality seemed to be numerically offset by immigration, similar to other populations. Because of the low survival rates of adult males and high emigration rates of subadult males, we suggest that the ability of the Black Hills population of mountain lions to withstand hunting is dependent on the population dynamics of adjacent populations, even though those populations are separated from the Black Hills by expanses of apparently unsuitable habitat. We suggest that South Dakota Game, Fish and Parks determine and anticipate potential changes in management goals of adjacent agencies and the implications of low survival rates and lack of recruitment of adult male mountain lions in the Black Hills population. What occurs in adjacent management districts likely influences the ability of the mountain lion population to withstand mortality within the Black Hills.

INTRODUCTION

Sport-hunting is a primary form of population management for mountain lions and is used by wildlife agencies to achieve a variety of objectives (Anderson et al. 2010). Despite the history and widespread use of sport-hunting mountain lions, published results that support success in reaching management objectives are lacking. Thus, scientists continue to suggest that the consequences of human-removal of mountain lions (e.g., depredation control, sport-hunting, public safety) are little understood and complex and therefore, sport-hunting should be minimal to lessen unintended consequences (Hornocker 2010).

Potential immediate effects of sport-hunting include changes in reproduction, survival, emigration/immigration, and population size. Reproduction could be altered through density-dependent mechanisms by allowing for greater resources, *per capita*, promoting higher body condition and greater reproductive output. However, litter sizes are similar for all studies in which cubs were counted in natal dens (<8 weeks old), regardless of hunting status (Cooley et al. 2009, Logan and Sweanor 2001, Spreadbury et al. 1996).

Contrary to increased productivity, decreased survival of cubs is an often speculated by-product of human-removals (Hemker et al. 1986, Ross and Jalkotzy 1992, Murphy et al. 1999, Cooley et al. 2009), because mountain lions exhibit some traits consistent with other infanticidal species (Logan and Sweanor 2001, Swenson 2003). Two studies found evidence that cub survival was higher in either protected areas or in areas receiving less hunting pressure, than in areas subjected to hunting (Cooley et al.

2009, Logan and Sweanor 2001). Logan and Sweanor (2001) found 6% lower survival in their 1-time experimentally treated area relative to their control area. Cooley et al. (2009) found cub survival was 50% lower in an area with sustained heavy harvest rates.

Dispersal and emigration has received little attention relative to consequences of sport-hunting, however, it is thought to be density-independent and likely not sensitive to manipulated densities of mountain lions (Logan and Sweanor 2001). Immigration has been found to at least partially compensate numerically for losses due to sport-hunting (Lindzey et al. 1994, Cunningham et al. 1995, Stoner et al. 2006, Robinson et al. 2008). However, immigration rates are likely to be highly dependent on connectivity with other populations (Stoner et al. 2006), such that increasing isolation would result in decreasing abilities to compensate for human-removals via immigration.

Adult survival is sensitive to sport-hunting. Adult survival is high for both sexes in protected populations (Logan and Sweanor 2001) and declines inversely with hunting-pressure (Stoner et al. 2006, Cooley et al. 2009). Adult males and females naturally exhibit differing survival rates (Cunningham et al. 1995, Logan and Sweanor 2001, Cooley et al. 2009); likely owing to differences in life-history strategies (Logan and Sweanor 2001). However, no studies have investigated whether removing established males results in higher contact rates between unfamiliar animals leading to increased rates of intraspecific strife and higher than expected mortality than due to sport-hunting alone.

Population density in mountain lions is a function of production and recruitment of females, immigration of males from other populations, and mortality. In studies where

human-removals were investigated, population density was lowered in relation to connectivity to other habitat (Stoner et al. 2006). Studies of mountain lions in relatively small study areas within vast areas of mountain lion habitat have concluded that despite low adult survival and high human-removal, densities remained unchanged due to immigration (Cunningham et al. 1995, Robinson et al. 2008). In study populations where the study area was disjunct to varying degrees from other mountain lion habitat, researchers documented temporary decreases in density, following high human-removals of mountain lions, but that density or population size returned to pre-removal densities following relaxation or cessation of high removal rates (Lindzey et al. 1992, Anderson and Lindzey 2005, Logan and Sweanor 2001, Stoner et al. 2006).

Our objectives were to document changes in population traits occurring coincident to the legalization of sport-hunting in a previously un hunted population. We hypothesized that litter sizes were dependent on prey density below a minimum level, with prey densities above a threshold allowing mountain lion litters to remain stable, regardless of mountain lion density. If litter sizes are prey density-dependent, then changes in mountain lion population density will not affect litter sizes. We hypothesized that cub survival is not density-dependent, but might be dependent on adult male survival. If cub survival is dependent on adult male survival, then declining adult male survival would result in declining cub survival, presumably due to social instability and increased infanticide. We expect that dispersal or emigration is density-independent and sport-hunting would not result in changes to these rates. If adult survival is sensitive to human-removal, then survival rates of both adult males and females would decline, with

males declining to a lower rate than females. We also expected to observe a stable numerical population, because sport-hunting was proposed to be conservative and within guidelines reported in the Cougar Management Guidelines (Cougar Management Guidelines Working Group 2005).

STUDY AREA

We studied the mountain lion population occupying the Black Hills Ecoregion (N44.09375°, W103.77691°) between 2002 and 2009. The Black Hills occupied about 14,600 km² and were entirely surrounded by the Northern Great Plains. Although genetic interchange does occur (Anderson et al. 2004), mountain lions in the Black Hills are semi-isolated from other populations in that they were surrounded by apparently unsuitable habitat and these long distances act to reduce immigration from adjacent areas. There was a small breeding population of mountain lions established on the Pine Ridge Escarpment about 48 km (shortest distance) to the south in Nebraska. Other breeding populations were 90 km northwest in the Custer National Forest (United States Forest Service), west of Broadus, Montana; 150 km southwest in the Laramie Range; 160 km west in the Big Horn Mountains, and 150 km north in the Badlands of North Dakota.

The Black Hills are an oblong-shaped complex of ridges, valleys, and steep canyons (Froiland 1990). Climate patterns in the Black Hills are characterized by hot summers and cold winters typical of a continental climate regime. The plant community was dominated by ponderosa pine (*Pinus ponderosa*) forests, but also contained spruce (*Picea glauca*), aspen (*Populus tremuloides*), and birch (*Betula* spp.) trees (Larson and Johnson 1999). Potential large prey species included white-tailed deer (*Odocoileus*

virginianus), mule deer (*O. hemionus*), elk (*Cervus elaphus*), American bison (*Bison bison*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*) as well as a variety of domestic livestock species. No other large carnivores were present in this system. Bobcat (*Lynx rufus*) and coyote (*Canis latrans*) are medium carnivores that occurred sympatrically with mountain lions.

The Black Hills lied within South Dakota (~65%) and Wyoming (~35%), USA. There were 4 areas where mountain lions are legally protected. Mount Rushmore National Memorial (~6 km²), Jewel Cave National Park (~5 km²), and Wind Cave National Park (~110 km²) were administered by the National Park Service. Custer State Park (~286 km²) was administered by the State of South Dakota. The Wyoming portion of the Black Hills was managed as a “population sink,” and high harvest rates were prescribed.

We defined our study area by the area fully encompassing all adult mountain lions radiocollared during this study, but truncated the area on the western side using the Wyoming-South Dakota state boundary. Our total study area encompassed 5,800 km², whereas the sampling area for population estimates spanned 5,400 km², because hunting (i.e., resampling) was not permitted in Custer State Park, Jewel Cave National Monument, Mount Rushmore National Monument, and Wind Cave National Park. The ecological population of mountain lions occupied the entire Black Hills ecoregion; however, we concentrated our capture efforts in South Dakota and we were unable to obtain sufficient numbers of radiocollared animals in Wyoming.

METHODS

Study Design

We divided the study period (2002–2010) into 2 timeframes; period 1 began 1 October 2002 and ended 30 September 2005 (2002–2005) and period 2 began 1 October 2005 and ended 30 December 2009 (2005–2009). Beginning 1 October 2005, the South Dakota Department of Game, Fish, and Parks initiated the first hunting season for mountain lions on the South Dakota side of the Black Hills, except in Custer State Park, Wind Cave National Park, Jewel Cave National Park, and Mt. Rushmore National Monument. Otherwise, the study population was subjected to the same department-removal protocols, whereby animals could be killed for depredation or public safety concerns during both periods. We focused capture efforts during all study periods in the portion of the Black Hills within South Dakota, where sport-hunting was authorized in 2005. We also captured animals within Custer State Park, where mountain lions were legally protected throughout the study period as a control following legalized hunting outside park boundaries.

We used the contiguous area of Custer State Park and Wind Cave National Park as a reference area (protected area). Although the protected area exhibits similar road densities and high daytime vehicle use, speed limits inside the area are low compared to roads outside the parks. The protected area had few human residences, no livestock, and no hunting of mountain lions was permitted during our study.

Captures

We captured mountain lions >3 months old using trained dogs (Hornocker 1970), foot-hold snares (Logan et al. 1999), foot-hold traps, wire-cage traps (Bauer et al. 2005), and free-dart (capture free-ranging animal by delivering immobilizing dart without prior restraint). We captured cubs <3 months by hand (Logan and Sweanor 2001). We restrained animals by placing in a burlap sack (e.g., cubs <3 months old) or by injecting captured animals with a mixture of telazol (tiletamine/zolazaline-hydrochloride, 4.84 mg/kg) and xylazine-hydrochloride (0.99 mg/kg, Kreeger 1996). We counteracted xylazine with yohimbine (0.125 mg/kg, Kreeger 1996). We aged captured animals using tooth-eruption, tooth-wear, eye color, and pelage characteristics (Currier 1983, Anderson and Lindzey 2000). We classified animals as cub (≤ 1 yr), subadult (1–3 yrs), and adult (≥ 3 years). We placed MOD-500 (Telonics, Mesa, Arizona) radiocollars on animals >9 months of age and expandable MOD-125 (Telonics, Mesa, Arizona) radiocollars on cubs that were >3 weeks of age. We attempted to capture our research animals in a random manner. All methods of capture have the possibility of sex- and age-specific bias due to differences in life-history traits, however we used multiple methods to reduce the potential for one method to bias our capture efforts. We tried to capture each animal that presented a trapping opportunity and when we used hounds, we released the hounds on the first trail we encountered in the area searched; thus we consciously attempted to be non-selective with respect to age or sex. Our capture and handling procedures followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were

approved by the South Dakota State University Institutional Animal Care and Use Committee (Approval No. 07-A024).

Litter Sizes and Sex Ratios

We located radiocollared adult females weekly using aerial telemetry. When ≥ 2 locations were within 500m from each other, we checked the area using ground telemetry the following day. If the radio signal indicated the animal was still present in the area, we approached the location of the animal by circling the suspected area until we could determine the precise location of the animal, by either sight or within a 60m-diameter circle. Once we determined the animal was using a specific den-site, we either displaced the animal by close approach with several people or preferably approached the den when the radio signal indicated the adult female was not present. Before entering the den-site, we visually determined the number of cubs present before disturbance and attempted to assess the age of the cubs, using visual cues (e.g., eye, ear, and tooth characteristics). When the cubs were estimated to be older than 3-weeks (eyes open, ears open and unfolded, deciduous teeth beginning to erupt, and stable while standing upright) we captured all individuals upon entering the den-site. We individually determined sex, age, and weight and applied ear-tattoos and eartags for each cub, while littermates were kept inside a burlap sack. Once all cubs were processed, we released the entire litter inside the den-site and left the area immediately.

We combined litters by study periods (period 1, 2002–2005; period 2, 2005–2009) but separated litters in period 2 by protected and hunted areas. We used analysis of variance (ANOVA) to test for differences in litter sizes by study period and area. We

compared the distribution of litter sizes in period 2 to those found in period 1 using a chi-squared test for independence. We used the proportion of litters containing 1, 2, 3, 4 cubs/litter during period 1 to calculate our expected values, and number of cubs in litters during period 2 as observed values. Additionally, we calculated expected values using distribution of cubs/litter found in an un hunted population in New Mexico, USA (Logan and Sweanor 2001). We calculated an overall sex ratio by adding the number of cubs for all captured litters by sex and calculated a sex ratio for each litter. We compared mean sex ratios using analysis of variance (ANOVA).

Survival

We collared all study animals with very high frequency radio-transmitters (VHF-collars, Telonics, Mesa, Arizona) outfitted with activity sensors (4-hour delay) or global positioning systems (GPS-collars, Northstar, King George, Virginia). We monitored signals to detect mortalities weekly. For animals with GPS-collars (subadult males), we assessed movement daily, however, because of the possibility an animal was remaining at a kill-site (Anderson and Lindzey 2005), we did not examine a cluster (i.e., 2 locations <100m apart over 1 or 2 nights) until 7 days had elapsed.

We calculated survival for cubs, subadults, and adults using the known-fate model in Program MARK (White and Burnham 1999). For cubs and subadults, we grouped animals by study period, but adults were grouped by year (Oct–Sep) and then years were grouped by study periods, for some analyses. We used sex and hunt status as covariates for all analyses. Only cubs that were initially captured ≤ 2 months old were used to calculate cub survival (Logan and Sweanor 2001). For subadults, we calculated a

mortality rate by following animals from independence until they emigrated from the study area or became residents. We calculated annual survival for adult animals from October to September each year. For some analyses, we defined non-hunted animals, as animals that occurred during period 1 or by use of protected areas, Custer State Park or Wind Cave National Park, during a portion of the year during period 2 (particularly during hunting seasons). We used program CONTRAST (Hines and Sauer 1989) to test for statistical differences in survival rates.

Cause of Mortality

When a radio signal indicated a potential mortality, we located the transmitter as soon as possible to verify a mortality event and determine the cause, if possible. If we could not determine cause of death by field evidence at the carcass, we shipped the animal to the Colorado State University Diagnostic Laboratory to determine if disease was a factor.

Compensatory Mortality

The South Dakota Department of Game, Fish, and Parks enumerates the known mortalities of all mountain lions, radiocollared and unmarked, annually. We used the documented mortalities to determine if the number of mountain lions lethally removed by state personnel, killed by motor vehicles, killed by other human-causes, and killed by natural causes declined when sport-hunting began in 2005. Other human-caused mortality included justified shooting by members of the public, illegal poaching, and accidental trapping during legal trapping activities. We used linear regression to analyze annual mortality by cause of death. We used *t*-tests to determine if the slope of the linear

regression line was different than zero. We hypothesized that if sport-hunting of mountain lions offset other mortality sources, then the slopes of linear regression lines would be negative. We used the linear regression of natural-caused mortalities as a reference.

Dispersal from Study Area or Population Emigration

We determined dispersal or emigration using aerial and GPS telemetry. We defined dispersal as the movement of an individual to areas outside of the study area and emigration as movement by an individual to areas outside the ecological population of mountain lions in the Black Hills Ecoregion. Because of the propensity of subadult animals to emigrate from the natal area (Logan and Sweaner 2001, Thompson 2009) and the Black Hills is an island of habitat, if a VHF-collared subadult animal was not located by the end of the study, we recorded the animal as having emigrated. However, if the radio signal from a VHF-collared adult animal was lost and not found by the end of the study, we censored the animal at last radio contact as a collar failure. We did not recover subadult male animals within our study area by mortality or capture activities, but many were returned to us from other areas as human-caused mortalities indicating survival during or post emigration. Whereas, we frequently recovered failed collars on subadult female or adult animals within our study area after a mortality event or during capture activities.

For subadult animals that survived, we used the known-fate model in Program MARK (White and Burnham 1999) to estimate dispersal and emigration rates. We coded the last contact or date of known emigration from GPS-collared animals as the terminal

event, where emigration was substituted for mortality. We began subadult encounter histories at 1 year of age and used monthly intervals until emigration, first litter born, or 3 years old, where the animal was considered to have survived to adult age.

Population Size

We used a 2-sample Lincoln-Peterson estimator (Williams et al. 2002) to calculate study population size for independent aged animals during 2005, 2006, 2007, 2009, 2010, coinciding with the annual mountain lion hunting season. We do not consider this to be an estimate of total population size, because not all areas of the Black Hills were represented by marked animals or by hunter-kills, particularly the southern and southwestern portions of the Black Hills, which are dominated by privately-owned land. Also, the Wyoming-side of the Black Hills is hunted and we had a few radiocollared animals using that area, we did not attempt to maintain radiocollars on the Wyoming-side and so, the number of marked animals was low. Our population estimate does not include the area encompassed by the contiguous Custer State Park-Wind Cave National Park or Jewel Cave and Mount Rushmore National Monuments, because animals within those areas were not available to hunters. The study area was useful, because all hunter-killed animals were obtained from within this study area and the area was stable throughout our study, so estimates should reflect the population size within the area.

We satisfied the assumption of population closure, by using short hunting seasons, which lasted 24, 19, 23, 45, and 41 days during the 5 seasons 2005–2010, respectively. Because our estimate does not include dependent young, only immigrating

animals must be considered to meet the population closure assumption. The Black Hills is largely isolated from other populations; although immigration does occur (Anderson et al. 2004). We used radiocollared individuals that died or emigrated from the study population to account for losses occurring during our population resampling periods. We found 0%, 0%, 1.9%, 3.3%, and 2% mortality of radiocollared animals occurring during our resampling periods, 2005–2010, respectively. We also documented 1.7% emigration of radiocollared animals during the 2009 hunting season. We accounted for these by scaling our estimate of availability for these animals by the proportion of days alive and present in the hunting area. For example, if an animal died on non-hunting causes on day 8 of a 45-day hunting season, we recorded this animal's availability as 0.178, instead of assuming availability as 1 or 0 (e.g., proportion available = $8/45 = 0.178$). Because some of our radiocollared animals occupied protected areas for all or part of the hunting seasons, we scaled each animal's availability by the proportion of locations outside of the protected areas that were recorded during each hunting season. For example, if 5 of 6 locations recorded indicated the animal was inside a protected-area, this animal only added 0.167 (e.g., proportion available = $1/6 = 0.167$) to the availability, rather than 1 or 0.

We used radiocollared animals that could be verified as located within the study area and alive as our marked sample (n_1) and hunter-killed animals as our resample (n_2). Hunters were not allowed to use trained hounds to hunt mountain lions and the consensus of hunters was they were not selective. Most hunters after killing a marked animal, indicated that they were not aware of the collar prior to killing the animal. We believed

that the assumption of equal-vulnerability to capture and recapture was satisfied in our study. All hunter-killed animals were required to be evaluated by South Dakota Department of Game, Fish, and Parks staff within 24 hours of death. During several years, hunters killed cubs and we excluded those animals from analysis, because we did not have a high number of cubs with radiocollars during all years. We included all animals killed on the South Dakota-side of the Black Hills ecoregion, including those animals that were killed on the periphery of the ecoregion that were not contained within the Black Hills hunting unit, defined by the state agency.

Population Composition

To reconstruct the population structure at time of resampling periods, we back-dated all captured animals to each resampling period. We assigned each animal that was present during the respective period as subadult (1–3 yrs) or adult (≥ 3 yrs), according to their estimated age at time of capture. Because of differential dispersal by sex (Thompson 2009), we coded females that were adults at capture, as having entered subadult status at 1 year of age and adult status at 3 years of age. Adult males that were captured were assumed to have entered the population as adults at 3 years of age. We back-dated harvested animals that were not previously marked and added them to the pool of known animals in the population, at time of resampling.

We calculated total population size for each year by partitioning the estimated number of independent animals into sex and age class by using the proportion of known animals for each year. We used the mean proportion of radiocollared adult females with

cubs and the mean number of cubs still alive at time of resampling, from 2007 and 2009 data, to estimate the number of dependent cubs for each year 2005 to 2009.

RESULTS

During period 1 (2002 – 2005), we captured 17 (4♀, 13♂), 16 (9♀, 7♂), and 16 (10♀, 6♂) cub (<1 yr), subadult (1–3 yrs), and adult (>3 yrs) mountain lions, respectively. During period 2 (2005-2009), we captured 103 (47♀, 56♂), 61 (27♀, 34♂) and 64 (40♀, 24♂) cub (<1 yr), subadult (1–3 yrs), and adult (>3 yrs) mountain lions, respectively.

Litter Sizes and Sex Ratios

We estimated mean litter sizes for un hunted animals in period 1 at 3.0 ($n = 8$, 95% CI 2.5–3.5), hunted animals in period 2 at 2.9 ($n = 26$, 95% CI 2.6–3.2), and protected animals in period 2 at 3.0 cubs/litter ($n = 4$, 95% CI 2.3–3.7). There was no evidence that litter sizes differed ($F_{2, 37} = 0.103$, 2-sided $P = 0.903$) between study groups.

Distribution of litter size did not differ between study periods ($\chi^2 = 0.69$, $df = 2$, 1-sided $P = 0.71$); however, proportionally more litters containing 2 cubs were found during period 2. In period 1, 25% ($n = 2$) of litters contained 2 cubs, 50% ($n = 4$) contained 3 cubs, and 25% ($n = 2$) contained 4 cubs. During period 2, 31% ($n = 8$) of litters contained 2 cubs, 50% ($n = 13$) contained 3 cubs, and 19% ($n = 5$) contained 4 cubs. The distribution of litter sizes during our hunting period did not differ from an un hunted population in New Mexico ($\chi^2 = 0.928$, $df = 2$, 1-sided $P = 0.629$; Logan and Sweanor 2001).

Of the 6 litters captured and sexed during period 1, there were 3 male-only (50%), 3 mixed-sex (50%), and 0 female-only litters (0%). Of the 25 litters captured in hunted areas in period 2, there were 5 male-only (20%), 15 mixed-sex (60%), and 5 female-only litters (20%). All 4 litters captured in protected areas during period 2 were mixed-sex.

Overall sex ratio (M:F) of litters captured in the natal den was 5.33:1 (16M, 3F), 0.89:1 (33M, 37F), and 1.40:1 (7M, 5F) for litters during period 1 and in hunted and protected areas of period 2, respectively. We found evidence that mean sex ratios of litters was different between study periods ($F_{(2, 34)} = 5.17$, 2-sided $P = 0.011$). Mean sex ratio (M:F) of litters was 1.21 ± 0.06 (SE), 1.0 ± 0.03 , and 1.05 ± 0.07 during period 1, and in hunted and protected areas in period 2, respectively.

Cub Survival (age 0–1 year)

During periods 1 and 2, we recorded the fates of 8 (6M, 2F) and 70 (36M, 34F) cubs that we first encountered ≤ 2 months of age. Over all years, male and female cubs exhibited similar mortality patterns and we found that cub mortality declined after 4 months of age to $<10\%$ (Figure 1.1).

We found survival was similar for cubs in areas subjected to human-removals (Table 1.1, $\chi^2 = 0.008$, $df = 1$, 2- sided $P = 0.928$). When we analyzed only the 2005–2009 cub survival, but split the data by animals residing in protected areas, we found that cubs in areas subjected to hunting had 47% lower survival than cubs in protected areas (Table 1.1, $\chi^2 = 6.233$, $df = 1$, 2- sided $P = 0.013$).

Subadult Survival (age 1–3 yrs)

We recorded survival of 16 (8M, 8F) and 66 subadult mountain lions (44M, 38F) until emigration or 3 years of age during periods 1 and 2, respectively. We found subadult survival declined was similar for both males and females from period 1 to 2 (excluding protected areas, Table 1.2), respectively (subadult male, $\chi^2 = 0.194$, $df = 1$, 2-sided $P = 0.660$; subadult female, $\chi^2 = 0.161$, $df = 1$, 2-sided $P = 0.689$). When we analyzed only the 2005–2009 subadult survival, but separated the data by animals residing in protected and hunt areas, we found that subadult males and females in areas subjected to hunting had 56% and 31% lower survival than conspecifics in protected areas (Table 1.2), respectively (subadult male, $\chi^2 = 1.764$, $df = 1$, 2-sided $P = 0.184$; subadult female, $\chi^2 = 1.583$, $df = 1$, 2-sided $P = 0.208$), however low sample sizes contributed to lack of statistical precision.

Subadult Dispersal from Study Area

We followed 10 (6M, 4F) and 40 (19M, 21F) subadults that survived to disperse from the study area or establish residence during period 1 and 2, respectively. During periods 1 and 2, subadult males dispersed from the study area at similar rates ($D_1 = 0.933$, $SE_1 = 0.15$, $n_1 = 6$, $D_2 = 0.980$, $SE_2 = 0.06$, $n_2 = 13$, $\chi^2 = 0.085$, $df = 1$, 2-sided $P = 0.771$). Subadult females also dispersed at similar rates between periods 1 and 2 ($D_1 = 0.209$, $SE_1 = 0.12$, $n_1 = 8$, $D_2 = 0.296$, $SE_2 = 0.13$, $n_2 = 22$, $\chi^2 = 0.242$, $df = 1$, 2-sided $P = 0.623$). Subadult males in hunted areas or protected areas dispersed at similar rates ($D_{\text{hunted}} = 0.980$, $SE_{\text{hunted}} = 0.06$, $n_{\text{hunted}} = 13$, $D_{\text{protected}} = 0.876$, $SE_{\text{protected}} = 0.15$, $n_{\text{protected}} = 6$, $\chi^2 = 0.414$, $df = 1$, 2-sided $P = 0.520$). Whereas, subadult females dispersed from protected

areas 45% less than conspecifics from hunted areas ($D_{\text{hunted}} = 0.296$, $SE_{\text{hunted}} = 0.13$, $n_{\text{hunted}} = 22$, $D_{\text{protected}} = 0.164$, $SE_{\text{protected}} = 0.10$, $n_{\text{protected}} = 5$, $\chi^2 = 0.648$, $df = 1$, 2- sided $P = 0.421$), however low sample sizes might have contributed to lack of statistical precision.

Subadult Emigration

We followed 10 (6M, 4F) and 40 (19M, 21F) subadults that survived to either emigrate from the Black Hills population or establish residence during period 1 and 2, respectively. We found emigration rates for both sexes of subadults were similar regardless of study period or protected status (Table 1.3). Subadult males emigrated at similar rates between study period 1 and 2 ($\chi^2 = 1.200$, $df = 1$, 2- sided $P = 0.273$). Subadult males subjected to hunting emigrated at similar rates compared to conspecifics that were not subjected to hunting ($\chi^2 = 0.851$, $df = 1$, 2- sided $P = 0.356$). Subadult females emigrated at similar rates between study periods 1 and 2 ($\chi^2 = 0.481$, $df = 1$, 2- sided $P = 0.488$). Subadult females subjected to hunting emigrated 42–46% more than conspecifics that were not subjected to hunting ($\chi^2 = 0.393$, $df = 1$, 2- sided $P = 0.531$), although small sample sizes contributed to lack of statistical precision.

Adult Survival (>3 years)

We recorded annual survival for 3–4 adult males and 6–11 adult females through study period 1. We recorded annual survival for 12–18 adult males and 21–47 adult females during period 2. We found that annual survival varied by years from 2002–2009 and generally declined for both sexes after 2005 (Figure 1.2, Figure 1.3).

When we combined years into study periods and separated animals in hunted areas and protected areas, we found dramatic differences in survival (Table 1.4). Annual adult male survival declined 43% from period 1 to period 2 ($\chi^2 = 5.365$, $df = 1$, 2- sided $P = 0.021$) and was 50% lower in hunted areas than in protected areas ($\chi^2 = 7.413$, $df = 1$, 2- sided $P = 0.007$). Annual adult female survival declined 13% from period 1 to period 2 ($\chi^2 = 4.061$, $df = 1$, 2- sided $P = 0.044$) and was 16% lower in hunted areas than in protected areas ($\chi^2 = 6.938$, $df = 1$, 2- sided $P = 0.008$).

Causes of Mortality

Cubs

From 2002 to 2005, we recorded 6 mortalities of cubs. We found 16.7% (SE = 15%) mortality due to humans and 83.3% (SE = 15%) was natural-caused. All natural mortality was attributed to infanticide. During 2005–2009, we recorded 29 mortalities, of which 21% (SE = 8%) was human-caused and 79% (SE = 8%) was natural-caused mortality. Natural-causes of mortality were infanticide (55%), with other causes being disease/malnutrition (10%), abandonment (7%), and accidents related to the mother (3%). We found similar distributions of mortalities between study periods ($\chi^2 = 0.45$, $df = 1$, 2- sided $P = 0.50$).

Subadults and Adults

From 2002 to 2005, we documented 10 deaths of radiocollared animals. We found 90% (SE = 9.5%) of mortality was human-caused (Table 1.5). From 2005 to 2009, we documented 82 deaths of radiocollared animals. We found 65% (SE = 5.3%) of mortality was human-caused (Table 1.5).

Human killing (e.g., department removal, hunting, poaching/trapping, excluding vehicle collisions) of animals was similar between study periods 1 and 2. During period 1 (2002–2005) and 2 (2005–2009), intentional human-caused mortality made up 60% (SE = 15.5%) and 54.0% (SE = 5.5) of all deaths of radiocollared animals, respectively. During periods 1 and 2, government-controlled mortality (e.g. department removal, hunting) increased from 30% (SE = 14.5%) to 46% (SE = 5.5%) of the radiocollared animal mortalities.

Compensatory Mortality

We found the number of documented mortalities generally increased over the study period from 8 in 2003 to 53 in 2009 (Table 1.6), largely due to the sport-hunting season. Natural-caused mortalities remained stable throughout the study period ($\text{slope}_{\text{natural-caused}} = 0.429 \pm 0.579$ (SE), $t = 0.74$, 2-sided $P = 0.492$; Figures 1.4, 1.5, 1.6). Number of mountain lions lethally-removed by state personnel increased over the study period ($\text{slope}_{\text{department-caused}} = 1.643 \pm 0.612$ (SE), $t = 2.68$, d.f. = 6, 2-sided $P = 0.044$; Figure 1.4). Number of mountain lions killed by documented motor vehicles and other human-causes remained stable throughout the study period ($\text{slope}_{\text{motor vehicle}} = -0.179 \pm 0.542$ (SE), $t = -0.33$, 2-sided $P = 0.755$, Figure 1.5; $\text{slope}_{\text{other human-caused}} = 0.357 \pm 0.291$ (SE), $t = 1.23$, 2-sided $P = 0.274$, Figure 1.6).

Population Size

Although in some years we did not have a large proportion of the population marked (n_1), nor did we resample a high proportion of the population (n_2), we found the population estimates were similar in 4 of 5 years from 2005–2010 (Table 1.7, Figure 1.7).

In 2007, of the 29 radiocollared adult females, there were 8 without cubs, 14 with cubs, and 7 were regarded as uncertain at the beginning of the resampling period (hunting season). Of the animals with known cub status, 64% were accompanied by cubs during the hunting season of 2007. In 2009, of the 31 radiocollared adult females, there were 2 without cubs, 14 with cubs, and the status of 15 were unknown. Of the animals with known cub status in 2009, 88% were accompanied by cubs during the hunting season of 2009. The mean number of cubs alive at the time of the resampling periods were 2.43 (SE = 0.272) and 2.33 (SE = 0.225) cubs/mother in 2007 and 2009, respectively. For both years combined, 74% of radiocollared adult females were accompanied by 2.38 cubs/adult female.

From 2005–2009, we estimated population sex and age class structure from 99, 108, 123, 123, and 77 animals known or assumed to have been in the population during each resampling period (hunting season, Table 1.8).

Total population estimates (including dependent cubs) ranged from 182–282 animals, excluding 2009 estimates (Table 1.9). We excluded the 2009 estimate because it was 2–3 times higher than the other 4 estimates and we suspected the estimate was inflated due to low number of collared animals killed during the 2009 hunting season (Table 1.9).

Considering the population estimate calculated during the first hunting season (October 2005) reflected the population size prior to the potential effects of hunting, the population did not decline significantly in subsequent years following legalized sport-hunting (Figure 1.7). However, the number of estimated adult males declined by 30%.

DISCUSSION

Litter Sizes and Sex Ratios

We found no indication that reproduction was affected by sport-hunting. Our litter sizes did not vary with study period or protected status and we found similar litter sizes to other studies that documented litters in natal dens (Logan and Sweanor 2001, Cooley et al. 2009). Cooley et al. (2009) also observed similar litter sizes independent of hunting pressure. Although we observed a difference in mean sex ratios of litters between study periods, the difference was likely an artifact of low sample size in period 1, where only 6 litters were captured and sexed.

Cub Survival (age 0–1 year)

Cub survival did not vary between study periods, but did vary within study period 2 by protected status. Low sample sizes in period 1 and human-removals of mountain lions (research accidents, depredation, public safety) during both periods might have contributed to the apparent similarities in cub survival by study period. However, cubs born inside Custer State Park (where human-removals did not occur) exhibited higher survival than those cubs born in areas where human-removals occurred, thereby corroborating previous research (Logan and Sweanor 2001, Cooley et al. 2009) indicating lower cub survival in populations subjected to human-removals.

Subadult Survival (age 1–3 yrs)

Subadult survival varied by sex, with subadult males exhibiting lower survival than females. The pattern of lower subadult male than female survival is consistent with findings of Logan and Sweanor (2001); survival of subadults declined as human removals

increased. We found lowest survival when animals were subjected to hunting and department removals (period 2, hunted areas), slightly higher survival when only subject to department removals (period 1), and highest survival in areas where human-removals did not occur (period 2, protected areas). In fact, subadult survival rates in our protected areas (subadult male, $S_{(i)} = 0.533$; subadult female, $S_{(i)} = 0.759$) were not unlike a protected population in central New Mexico, where subadult male and female survival was 0.56 and 0.88, respectively (Logan and Sweanor 2001).

Subadult Dispersal from Study Area and Emigration

We developed 2 metrics to describe the tendency of juvenile mountain lions to leave the natal area or population. We used our functional study area to calculate dispersal rates and the ecological population to describe emigration rates. We used these metrics because most studies of mountain lions have been conducted in small study areas relative to the total ecological population in the respective area. Few studies have been conducted on the ecological population level, where the study area was surrounded by varying distances of non-habitat (Logan and Sweanor 2001). The ecological population concept is most similar to our study population and we documented that not all juvenile males emigrate. Subadult male emigration from the Black Hills ecological population occurred at 76–94%; similar to rates calculated in New Mexico (83%; Sweanor et al. 2000). Fewer subadult females emigrated (12–22%) than was observed in New Mexico (33–59%; Sweanor et al. 2000).

We also found evidence that emigration might be density-dependent at low threshold densities. We found 6 males that settled within the ecological population. All

of these individuals settled on the Wyoming-portion of the Black Hills. The Wyoming Black Hills is managed intensively to create a “sink population” in an effort to reduce depredation complaints and compensation payments (J. Sandrini, Wyoming Game and Fish Department, Newcastle, Wyoming, *personal communication*). In that area, the quota is set high relative to the anticipated population. In fact, none of 6 radiocollared males that moved to the Black Hills of Wyoming survived more than 2 years past adulthood and 5 of 6 were killed by hunters. Yet, we observed no males establishing residences on the South Dakota-portion of the Black Hills, where the population remained stable during our study.

Adult Survival (>3 years)

Survival of adults appears to be sensitive to human-removals, with adult males being most sensitive. In areas subjected to department removals only, survival rates of both males and females were slightly lower than protected areas, but when hunting was added, survival declined precipitously in the adult males. Other mountain lion populations subjected to hunting exhibited similar survival rates with rates of 0.36–0.45 calculated for adult males (Cunningham et al. 1995, Stoner et al. 2006, Cooley et al. 2009). Survival rates for adult females in populations with high human-removals were 0.66 and 0.79 (Cunningham et al. 1995, Cooley et al. 2009), and were similar to our study as well.

Compensatory Mortality

We found no evidence that increased mortality due to sport-hunting offset mortality due to other factors. The number of mountain lions lethally-removed by state

personnel continued to increase in years of sport-hunting, despite apparent numerical stability in the mountain lion population. The increased number of lethal-removals might reflect decreasing public tolerance or conflicts between interest groups (e.g. government, preservationist, utilitarian; Mattson et al. 2010). We documented stability in the number of mountain lions that died annually to motor vehicle collisions, other human-causes, and natural-causes throughout the study period. Motor vehicle collisions with mountain lions might be a random source of mortality and would reflect the numerical stability of the population that we documented.

Population Size

The population estimate for the sampling area varied little from 107–136 independent animals, excluding 2009. Hunting mortality varied from 0-16% (mean = 8.4, SE = 4.6), 5–21% (mean = 12.7, SE = 4.6), 11–50% (mean = 33.6, SE = 11.9), and 4–18% (mean = 12.8, SE = 4.6) of the estimated adult males, adult females, subadult males, and subadult females in the sampling area, respectively. The fact that the population remained stable is not surprising. Populations with a harvest of 40% of the adult population declined significantly (Stoner et al. 2006), whereas a population with 24% hunting mortality did not decline (Robinson et al. 2008). Despite stability in population size, the number of adult males apparently declined over time and the number of adult females remained stable.

Population Estimate Concerns

We estimated the population in the functional study area in each of 5 years. Four of five estimates were similar, whereas the 2009 estimate was >3 times higher. The 2009

estimate was likely inflated due to a low number of radiocollars harvested by hunters, despite the highest number of radiocollars available (Figure 1.8). However, after excluding the 2009 population estimate, the data indicated the population was higher in 2010, despite the very low survival rate of all segments of the population except adult females. Harvest data can not be used to determine the true population composition because harvest might reflect relative vulnerability to hunters (Anderson and Lindzey 2005). Although we had high numbers of radiocollared animals during some of the hunting seasons (e.g., 2006, 2007, 2009, 2010), the number in 2005 might have been too low to estimate the population.

Also, the number and composition of radiocollared animals in 2010 was biased by mortality rates. We continuously captured mountain lions throughout each year beginning July 2006 through June 2009; thus, composition of radiocollars would not be biased by mortality rates, however we ceased capturing animals from July to December 2009 and therefore the numbers of radiocollared animals declined proportional to the sex- and age-specific mortality rates. We back-dated all animals obtained by research or hunters to obtain a large sample to estimate composition, which benefitted the estimates of individual population components in all years, except the final estimate 2010. Since the composition of the 2010 estimate was biased by lack of continuous captures and did not benefit from future captures, the total population estimate based on 2010 composition was biased. If we used the population composition for the last unbiased year (2009), we obtain a 2010 population estimate of 215, rather than 282. Thus, the conclusion would be

that the study population remained largely stable or grew by 15% from 2006 to 2010 (minimum = 182, maximum = 215).

Immigration

For the population to have remained stable, decreased emigration or increased immigration must have occurred. We followed 25 males that were known to have been born on the South Dakota side of the Black Hills. Of these 25, only 6 were found to establish home areas within the Black Hills population, however, all of these animals settled in Wyoming, outside the study area. Therefore, these animals did not contribute to the population estimate. Through genetic work, Anderson et al. (2004) suggested that 35.3 individuals immigrate into the Black Hills per generation, however actual estimates of immigration rates do not exist. Thus, the ability of adult male mountain lions in the Black Hills to withstand mortality remains unknown. Wyoming Game and Fish Department managed the west side of the Black Hills as a “population sink” to reduce depredation complaints and subsequent compensation payments. No mountain lions were originally collared on the Wyoming-side and we have no data to suggest that any animals on the South Dakota-side originated from the Wyoming-side. Nevertheless, subadult males have been collared and observed emigrating over long-distances (Thompson and Jenks 2005). Thus, if this occurs in other populations (Stoner et al. 2007), then it is possible that a higher than expected rate of immigration into the Black Hills is occurring that compensated for adult males dying from all causes.

MANAGEMENT IMPLICATIONS

Our study corroborated other studies and adds additional support to the growing body of knowledge regarding the influences of human-removal on population dynamics of mountain lions. For practical purposes, reproduction was density-independent and can not be relied upon to compensate for hunting mortality on a scale typical of management units in the western USA. Dispersal might be density-dependent; however, the threshold appears to be low and given the overwhelming body of evidence under normal hunting rates in the western USA, recruitment via reproduction can not be expected to maintain adult male population components. Successful immigration appears imperative to maintaining populations and future hunting opportunities (if desired), however, connectivity likely plays a strong role. Immigration is likely dependent on connectivity and the dynamics (management) of populations long-distances away. For immigration to occur into the Black Hills, managers in Wyoming, Colorado, and Montana must consider the implications of their regimes on other populations. Given local politics and sovereignty of individual states, considerations beyond state boundaries are unlikely, although highly relevant.

Although numerically capable of withstanding even high rates of human removals, social stability of mountain lions appears sensitive to harvest in the Black Hills. Survival of all ages appears to be inversely related to intensity of human-removals of mountain lions. Survival rates of cubs and subadults possibly declined as a function of turnover in adult males. Adult males appeared to be most sensitive to human-removal rates, where their survival rates can decline to very low levels. Adult males being more

susceptible seems related to competition with conspecifics, where removing adult males might elicit cascading mortalities into cub-, subadult, and adult male-components of populations.

LITERATURE CITED

- Anderson, C. R., Jr., and F. G. Lindzey. 2000. A guide to estimating mountain lion age classes. Wyoming Cooperative Fish and Wildlife Research Unit: Laramie, Wyoming, USA.
- Anderson, C. R., Jr., and F. G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. *Wildlife Society Bulletin* 33:179–188.
- Anderson, C. R., Jr., F. G., Lindzey, and D. B. McDonald. 2004. Genetic structure of cougar populations across the Wyoming Basin: metapopulation or megapopulation. *Journal of Mammalogy* 85:1207–1214.
- Anderson, C. R., Jr., F. G. Lindzey, K. H. Knopff, M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41 – 54 *in* M. Hornocker, and S. Negri, eds. *Cougar ecology and conservation*. The University of Chicago Press, Chicago, USA.
- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *The Southwestern Naturalist* 50:466–471.
- Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology* 90:2913–2921.

- Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines, WildFutures, Bainbridge, WA.
- Cunningham, S. C., L. A. Haynes, C. Gustavson, and D. D. Haywood. 1995. Evaluation of the interaction between mountain lions and cattle in the Aravaipa-Klondyke area of southeast Arizona. Arizona Game and Fish Department Research Branch Technical Report No. 17. Phoenix, Arizona, USA.
- Currier, M. J. P. 1983. *Felis concolor*. Mammalian Species 200:1–7.
- Froiland, S. G. 1990. Natural history of the Black Hills and Badlands. The Center for Western Studies, Sioux Falls, South Dakota, USA.
- Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.
- Hemker, T. P., F. G. Lindzey, B. B. Ackerman, and A. J. Button. 1986. Survival of cougar cubs in a non-hunted population. Pages 327–332 in S. D. Miller, and D. D. Everett. Cats of the world: biology, conservation, and management. The National Wildlife Federation, Washington, DC, USA.
- Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST – a general program for the analysis of several survival or recovery rate estimates. United States Fish and Wildlife Service Technical Report 24, Washington, DC. Available online at <http://mbr-pwrc.usgs.gov/software.html>

- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* 21.
- Hornocker, M. 2010. Pressing business. Pages 235 – 247 *in* M. Hornocker, and S. Negri, eds. *Cougar ecology and conservation*. The University of Chicago Press, Chicago, USA.
- Kreeger, T. J. 1996. *Handbook of wildlife chemical immobilization*. International Wildlife Veterinary Services. Laramie, Wyoming, USA.
- Larson, G. E., and J. R. Johnson. 1999. *Plants of the Black Hills and Bear Lodge Mountains: a field guide with color photographs*. Fenske Media Corporation, Rapid City, SD, USA.
- Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. *Journal of Wildlife Management* 58:619–624.
- Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Population response to manipulation in southern Utah. *Wildlife Society Bulletin* 20:224–227.
- Logan, K. A., L. L. Sweanor, J. F. Smith, and M. G. Hornocker. 1999. Capturing pumas with foot-hold snares. *Wildlife Society Bulletin* 27:201–208.
- Logan, K. A., and L. L. Sweanor. 2001. *Desert puma: evolutionary ecology of an enduring carnivore*. Island Press, Washington, DC, USA.

- Logan, K. A., and L. L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105–117 *in* M. Hornocker, and S. Negri, eds. *Cougar ecology and conservation*. The University of Chicago Press, Chicago, USA.
- Mattson, D. J., and S. G. Clark. 2010. People, Politics, and Cougar Management. Pages 206–220 *in* M. Hornocker, and S. Negri, eds. *Cougar ecology and conservation*. The University of Chicago Press, Chicago, USA.
- Murphy, K. M., P. I. Ross, and M. G. Hornocker. 1999. The ecology of anthropogenic influences on cougars. Pages 77–101 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, eds. *Carnivores in ecosystems: the Yellowstone experience*. Yale University Press, New Haven, CT, USA.
- Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* 18:1028–1037.
- Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. *Journal of Wildlife Management* 56:417–426,
- Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. *Journal of Wildlife Management* 64:962–969.
- 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 Wildlife Management* 72:933–939.

- Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. *Journal of Wildlife Management* 70:1588–1600.
- Sweaner, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798–808.
- Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171 – 189 *in* M. Festa-Bianchet, and M. Apollonio, eds. *Animal behavior and wildlife conservation*. Island Press, Washington, DC, USA.
- Thompson, D. J. 2009. Population demographics of cougars in the Black Hills: survival, dispersal, morphometry, genetic structure, and associated interactions with density-dependence. Dissertation. South Dakota State University, Brookings, South Dakota, USA.
- Thompson, D. J., and J. A. Jenks. 2005. Long-distance dispersal by a subadult male cougar from the Black Hills, South Dakota. *Journal of Wildlife Management* 69:818–820.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, New York, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–139.

Table 1.1. Survival rates for mountain lion (*Puma concolor*) cubs (<1 yr) from birth until independence in the Black Hills, South Dakota, 2002–2009. All cubs were captured in the natal den and were <8 weeks of age. The study area was subdivided by time (study period 1 and 2) and place (hunted, protected). During study period 1, no mountain hunting was permitted, except for depredation and public safety and those animals were controlled by agency personnel. During study period 2, mountain lions hunting was legal in most of the study area, and was not permitted in certain protected areas, notably Custer State Park and Wind Cave National Park.

Sex	Study Period	Area	<i>n</i>	$S_{(i)}$	SE
Male	1	Not Hunted	6	0.488	0.179
Male	2	Hunted	29	0.494	0.087
Male	2	Protected	7	0.822	0.116
Female	1	Not Hunted	2	0.536	0.197
Female	2	Hunted	29	0.541	0.088
Female	2	Protected	5	0.849	0.107
Both sexes	1	Not Hunted	8	0.500	0.177
Both sexes	2	Hunted	58	0.517	0.066
Both sexes	2	Protected	12	0.833	0.108

Table 1.2. Annual survival rates for subadult (1–3 yrs of age) mountain lions (*Puma concolor*) in the Black Hills, South Dakota, 2002–2009. All animals were captured as cubs or estimated to be within the age class at original capture. The study area was subdivided by time (study period 1 and 2) and place (hunted, protected). During study period 1, no mountain hunting was permitted, except for depredation and public safety and those animals were controlled by agency personnel. During study period 2, mountain lions hunting was legal in most of the study area, and was not permitted in certain protected areas, notably Custer State Park and Wind Cave National Park.

Sex	Study Period	Area	<i>n</i>	$S_{(i)}$	SE
Male	1	Not Hunted	8	0.319	0.16
Male	2	Hunted-only	28	0.236	0.10
Male	2	Protected-only	8	0.533	0.20
Female	1	Not Hunted	8	0.604	0.15
Female	2	Hunted-only	22	0.527	0.12
Female	2	Protected-only	5	0.759	0.14

Table 1.3. Emigration rates for subadult (1–3 yrs of age) mountain lions (*Puma concolor*) in the Black Hills, South Dakota, 2002–2009. Emigration was defined as movement by an individual to areas outside of the ecological population occupying the entire Black Hills ecoregion. The study area was subdivided by time (study period 1 and 2) and place (hunted, protected). During study period 1, no mountain hunting was permitted, except for depredation and public safety and those animals were controlled by agency personnel. During study period 2, mountain lions hunting was legal in most of the study area, and was not permitted in certain protected areas, notably Custer State Park and Wind Cave National Park.

Sex	Study Period	Area	<i>n</i>	$E_{(i)}$	SE
Male	1	Not Hunted	6	0.759	0.15
Male	2	Hunted-only	13	0.936	0.06
Male	2	Protected-only	6	0.787	0.15
Female	1	Not Hunted	4	0.121	0.09
Female	2	Hunted-only	18	0.225	0.12
Female	2	Protected-only	3	0.131	0.09

Table 1.4. Annual survival rates for adult (≥ 3 yrs of age) male and female mountain lions (*Puma concolor*) in the Black Hills, South Dakota, 2002–2009. The study area was subdivided by time (study period 1 and 2) and place (hunted, protected). During study period 1, no mountain hunting was permitted, except for depredation and public safety and those animals were controlled by agency personnel. During study period 2, mountain lions hunting was legal in most of the study area, and was not permitted in certain protected areas, notably Custer State Park and Wind Cave National Park.

Sex	Study Period	Area	<i>n</i>	<i>S</i> _(i)	SE
Male	1	Not Hunted	5	0.703	0.11
Male	2	Hunted-only	27	0.401	0.07
Male	2	Protected-only	5	0.803	0.13
Female	1	Not Hunted	11	0.904	0.04
Female	2	Hunted-only	59	0.790	0.04
Female	2	Protected-only	10	0.939	0.04

Table 1.5. Cause-specific mortality of radiocollared mountain lions (*Puma concolor*) in the Black Hills, South Dakota, 2002–2009. The study period was subdivided into 2 periods. Mountain lion hunting was not permitted 2002–2005, and was legal 2005–2009. During both study periods mountain lions were lethally controlled for livestock depredation and public safety concerns.

Cause	Period	<i>n</i>	Mean (%)	SE	95% Confidence Interval	
					lower	upper
Accident/Injury/Drowning	1	1	10.0	9.5	1.8	40.4
Accident/Injury/Drowning	2	3	3.7	2.1	1.3	10.2
Disease/Old-age/Unknown	1	0	0	0	0	27.8
Disease/Old-age/Unknown	2	13	15.9	4.0	9.5	25.3
Intraspecific Strife	1	0	0	0	0	27.8
Intraspecific Strife	2	13	15.9	4.0	9.5	25.3
Department Removal	1	3	30	14.5	10.8	60.3
Department Removal	2	13	15.9	4.0	9.5	25.3
Hunting	1	0	0	0	0	27.8
Hunting	2	25	30.5	5.1	21.6	41.1

Table 1.5. continued

Cause	Period	<i>n</i>	Mean	SE	95% Confidence Interval	
			(%)		lower	upper
Poaching/Trapping	1	3	30	14.5	10.8	60.3
Poaching/Trapping	2	6	7.3	2.9	3.4	15.1
Research Accident	1	2	20	12.6	5.7	51.0
Research Accident	2	7	8.5	3.1	4.2	16.6
Vehicle Collision	1	1	10.0	9.5	1.8	40.4
Vehicle Collision	2	2	2.4	1.7	0.7	8.5
Natural-caused	1	1	10	9.5	1.8	40.4
Natural-caused	2	29	35.4	5.3	25.9	46.2
Human-caused	1	9	90	9.5	59.6	98.2
Human-caused	2	53	64.6	5.3	53.8	74.1

Table 1.6. Number of mountain lions that died annually from 2003 – 2009 in the Black Hills of South Dakota.

Year	Cause of Death	No. Individuals	Proportion of Total (%)
2003	Department Removal	3	38
	Motor Vehicle	1	13
	Other Human-caused	1	13
	Legal Hunting	0	0
	Natural-caused	3	38
2004	Department Removal	6	38
	Motor Vehicle	8	50
	Other Human-caused	2	13
	Legal Hunting	0	0
	Natural-caused	0	0

Table 1.6. continued

Year	Cause of Death	No. Individuals	Proportion of Total (%)
2005	Department Removal	8	25
	Motor Vehicle	7	22
	Other Human-caused	1	3
	Legal Hunting	14	44
	Natural-caused	2	6
2006	Department Removal	13	30
	Motor Vehicle	7	16
	Other Human-caused	5	12
	Legal Hunting	16	37
	Natural-caused	2	5

Table 1.6. continued

Year	Cause of Death	No. Individuals	Proportion of Total (%)
2007	Department Removal	8	17
	Motor Vehicle	6	13
	Other Human-caused	4	9
	Legal Hunting	19	41
	Natural-caused	9	20
2008	Department Removal	8	47
	Motor Vehicle	3	18
	Other Human-caused	4	24
	Legal Hunting	1	6
	Natural-caused	1	6

Table 1.6. continued

Year	Cause of Death	No. Individuals	Proportion of Total (%)
2009	Department Removal	17	32
	Motor Vehicle	3	6
	Other Human-caused	2	4
	Legal Hunting	27	51
	Natural-caused	4	8

Table 1.7. Number of estimated independent (>1 yr of age) mountain lions (*Puma concolor*) in the sampling area in the Black Hills, South Dakota. Estimates were derived from 2-sample Lincoln–Peterson, mark-recapture analysis by using the number of mountain lions with functioning radiocollars at the beginning of the resampling period (n_1) and the number of radiocollared (m_2) and total (n_2) mountain lions killed by hunters during the resampling period. These estimates do not include dependent cubs (<1 yr of age) or animals outside of the sampling area, which was defined as the area encompassed by mountain lion captures for research and mountain lions killed by hunters.

Year	$N_{\text{independent}}$	SE	95% Confidence Interval		Density* Animals/100 km ²	n_1	n_2	m_2	Proportion of N marked	Proportion of N resampled
			lower	upper						
2005	125	36	55	195	2.3	9.600	13	1	0.077	0.104
2006	107	29	50	165	2.0	26.780	16	4	0.250	0.149
2007	117	28	62	171	2.2	38.838	18	6	0.333	0.154
2009	346	108	134	558	—	41.516	25	3	0.120	0.072
2010	136	28	81	191	2.5	33.009	37	9	0.243	0.273

* estimated density based on 5400 km² study area; excludes Custer S. P. / Wind Cave N. P.

Table 1.8. Sex and age composition of the independent mountain lion (*Puma concolor*) population present in the sampling area in the Black Hills, South Dakota during the respective hunting period for each year. The number of animals is based on back-dating adult and subadult animals from time of research capture or harvest based on estimated ages. Adult males were only back-dated until 3 yrs of age, whereas adult females were back-dated until 3 yrs of age as adults, and 1–3 yrs of age as subadults. Sex and age classes are subadult male (1–3 yrs of age, SM), adult male (≥ 3 yrs of age, AM), subadult female (SF), and adult female (AF).

Year	No. SM	No. AM	No. SF	No. AF	Total	%SM	%AM	%SF	%AF
2005	8	17	43	32	99	8	17	43	31
2006	10	19	36	43	108	9	18	33	40
2007	20	16	41	46	123	16	13	33	37
2009	21	19	42	41	123	17	15	34	33
2010	12	8	10	47	77	16	10	13	61

Table 1.9. The number of mountain lions (*Puma concolor*) by sex and age class and estimated total number of mountain lions present in the sampling area in the Black Hills, South Dakota, at the beginning of each respective hunting period, including dependent cubs (<1 yr of age). Numbers of SM, AM, SF, and AF were calculated by using proportion of the estimated number of independent animals and population composition data determined by back-dating captured animals to reconstruct the population. Number of cubs was determined by using the mean number of radiocollared adult females known to have cubs during the hunting seasons of 2007 and 2009 and the mean number of cubs present with each radiocollared adult female. Sex and age classes are subadult male (1–3 yrs of age, SM), adult male (≥ 3 yrs of age, AM), subadult female (SF), adult female (AF), and cubs (0–1 yr of age, C).

Year	No. SM	No. AM	No. SF	No. AF	No. C	N_{total}
2005	10	21	54	39	69	194
2006	10	19	36	43	75	182
2007	19	15	39	44	77	193
2009	59	53	118	115	203	549
2010	21	14	18	83	146	282

Figure 1.1. Survival curve for mountain lion (*Puma concolor*) cubs (<1 yr of age) in the Black Hills, South Dakota, 2005–2009. Survival estimates are based on radiotelemetry of marked animals that were marked in the natal den and were estimated to be <8 weeks of age. Survival rates were calculated by using the product-limit estimator (Kaplan and Meier 1958). Although each cub was not born at the same time, each cub was entered at the estimated age in weeks, regardless of the timing of birth.

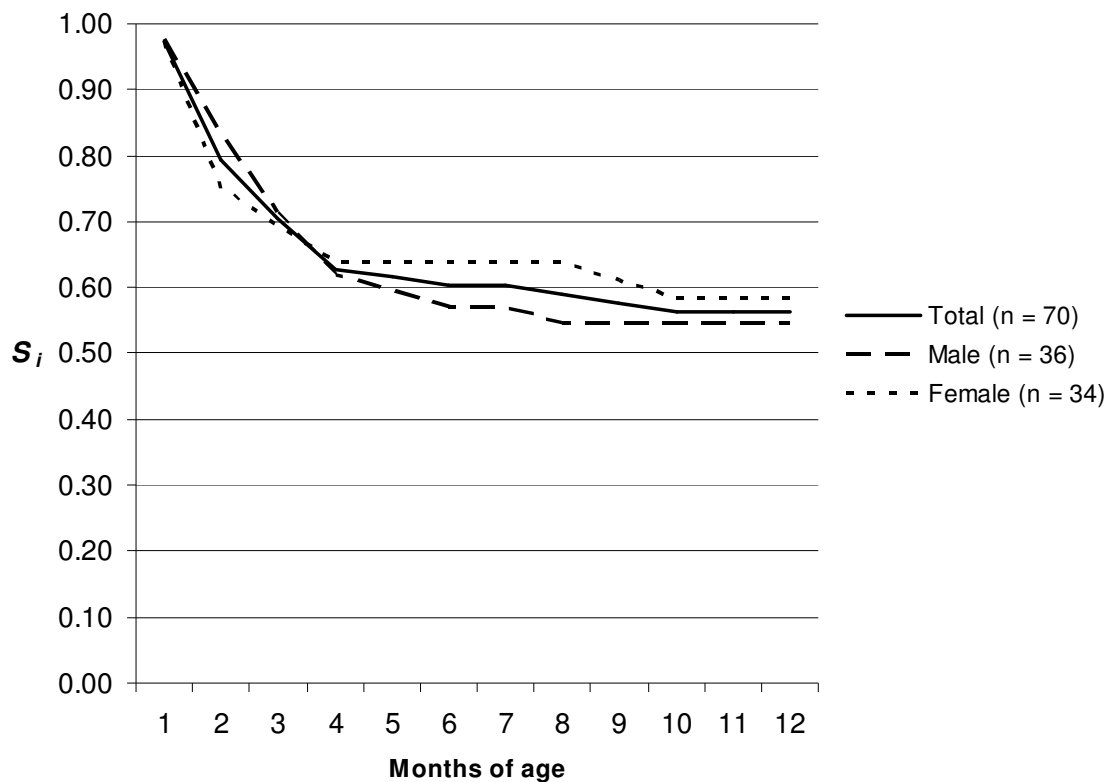


Figure 1.2. Annual survival estimates for adult male mountain lions (*Puma concolor*) in the Black Hills, South Dakota. Hunting of mountain lions began between the 2004–2005 and 2005–2006 years.

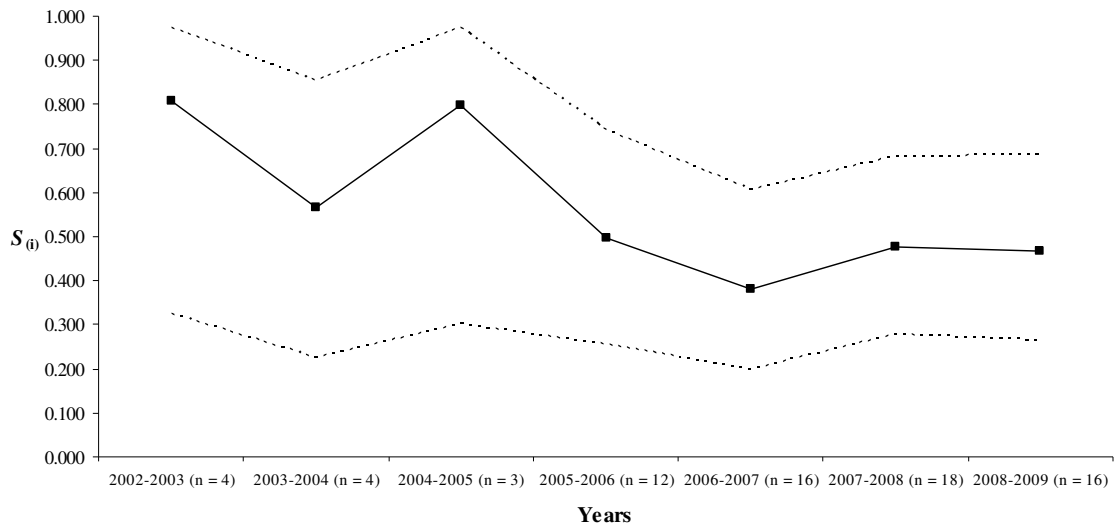


Figure 1.3. Annual survival estimates for adult female mountain lions (*Puma concolor*) in the Black Hills, South Dakota. Hunting of mountain lions began between the 2004–2005 and 2005–2006 years.

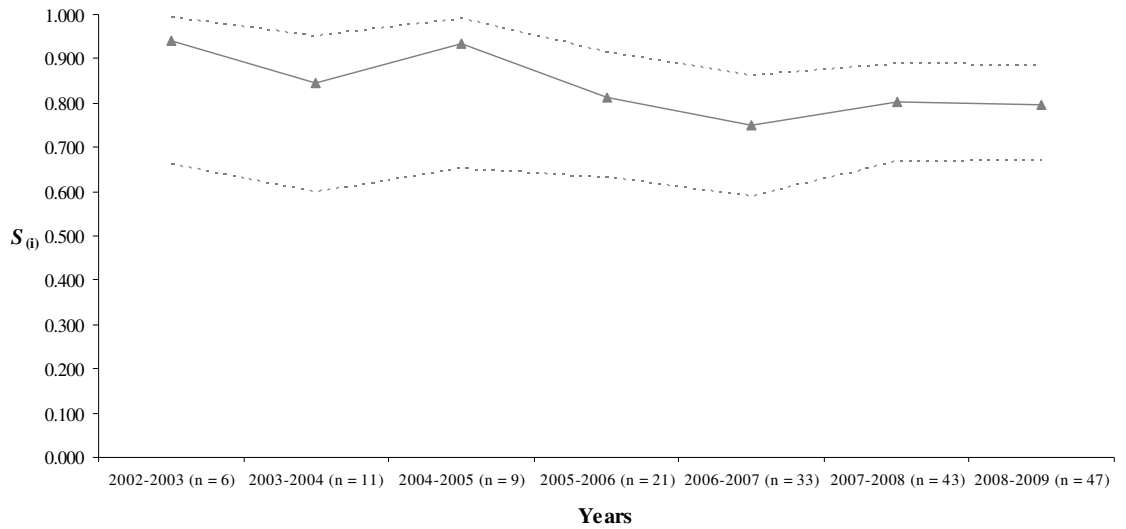


Figure 1.4. Number and linear regression of mountain lions (*Puma concolor*) that were lethally removed by South Dakota Department of Game, Fish, and Parks, as well as those that died by natural causes from 2003 – 2009 in the Black Hills of South Dakota.

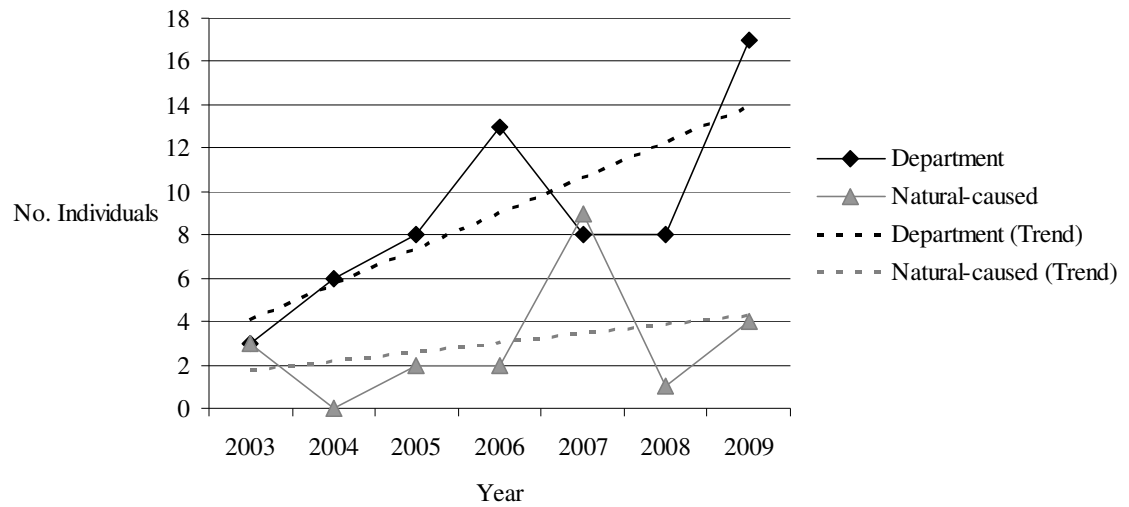


Figure 1.5. Number and linear regression of mountain lions (*Puma concolor*) that were killed in motor vehicle collisions, as well as those that died by natural causes from 2003 – 2009 in the Black Hills of South Dakota.

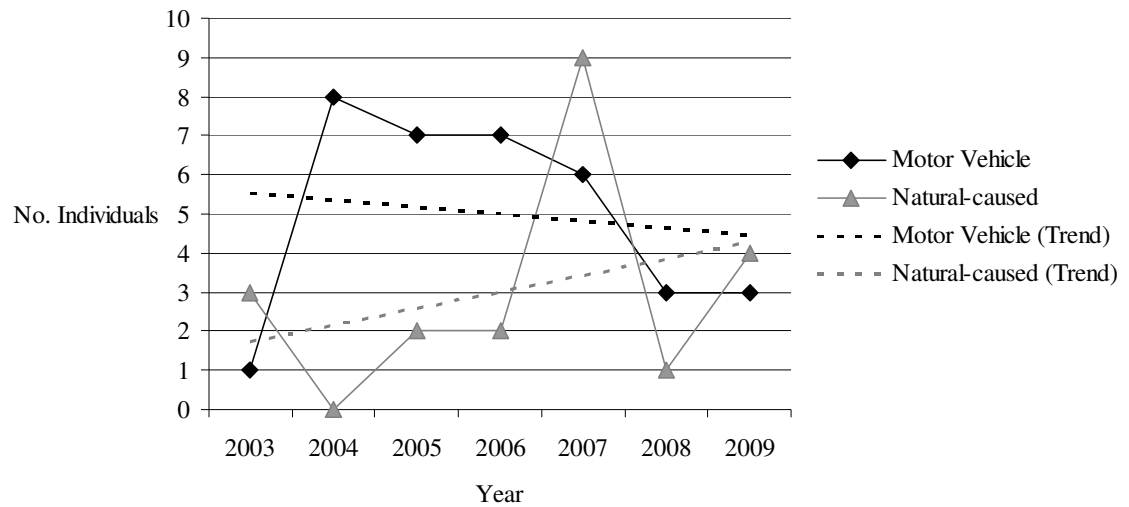


Figure 1.6. Number and linear regression of mountain lions (*Puma concolor*) that were killed by other human causes (e.g., justified public shooting, poaching, incidental trapping), as well as those that died by natural causes from 2003 – 2009 in the Black Hills of South Dakota.

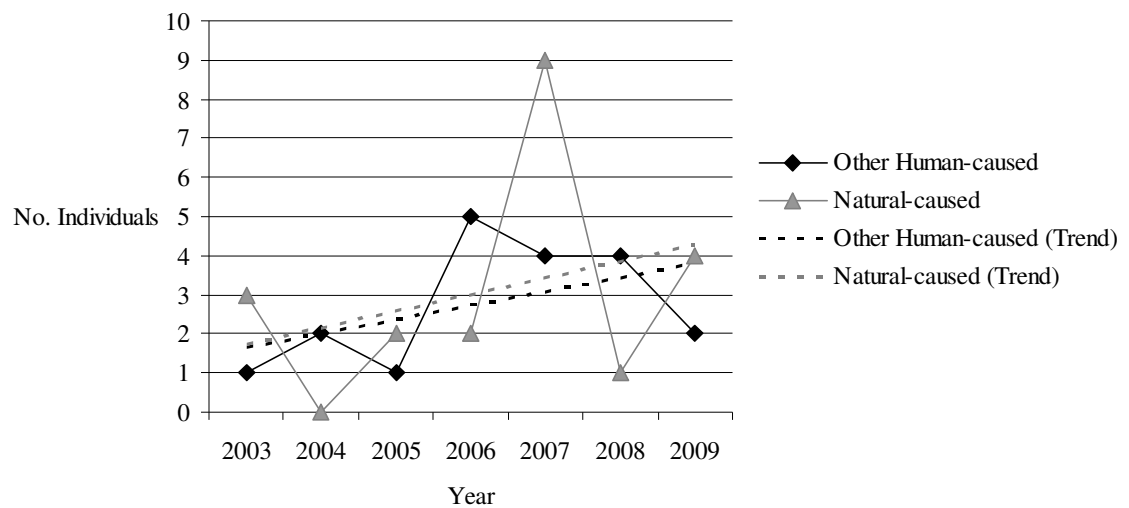


Figure 1.7. Estimated number of independent mountain lions (*Puma concolor*) in the sampling area in the Black Hills, South Dakota, based on 2-sample Lincoln–Peterson mark-recapture analysis.

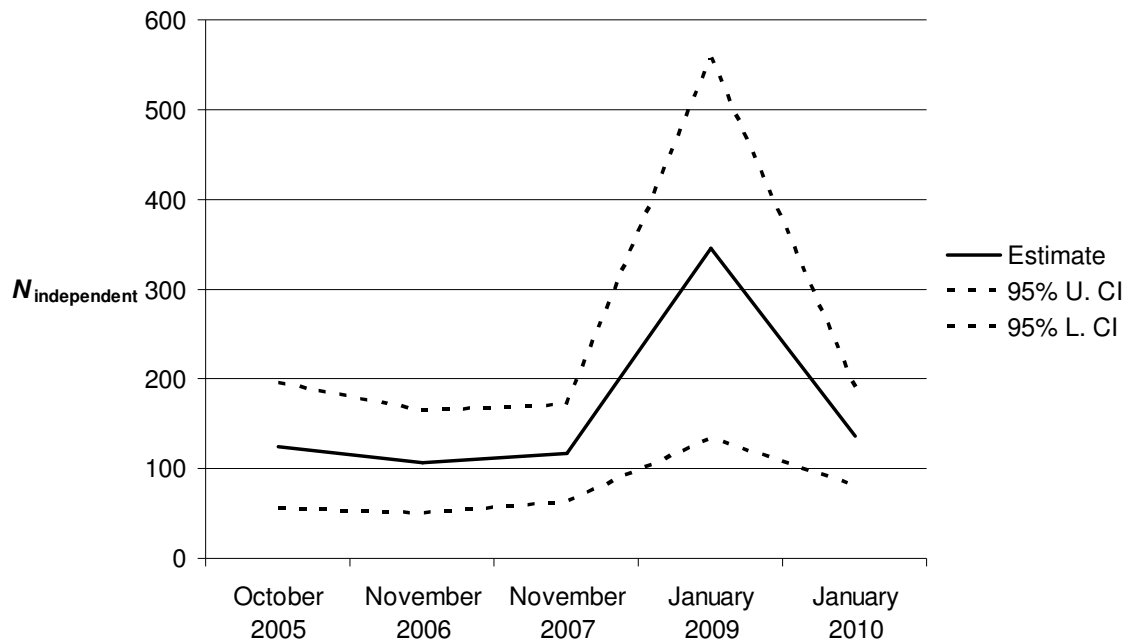
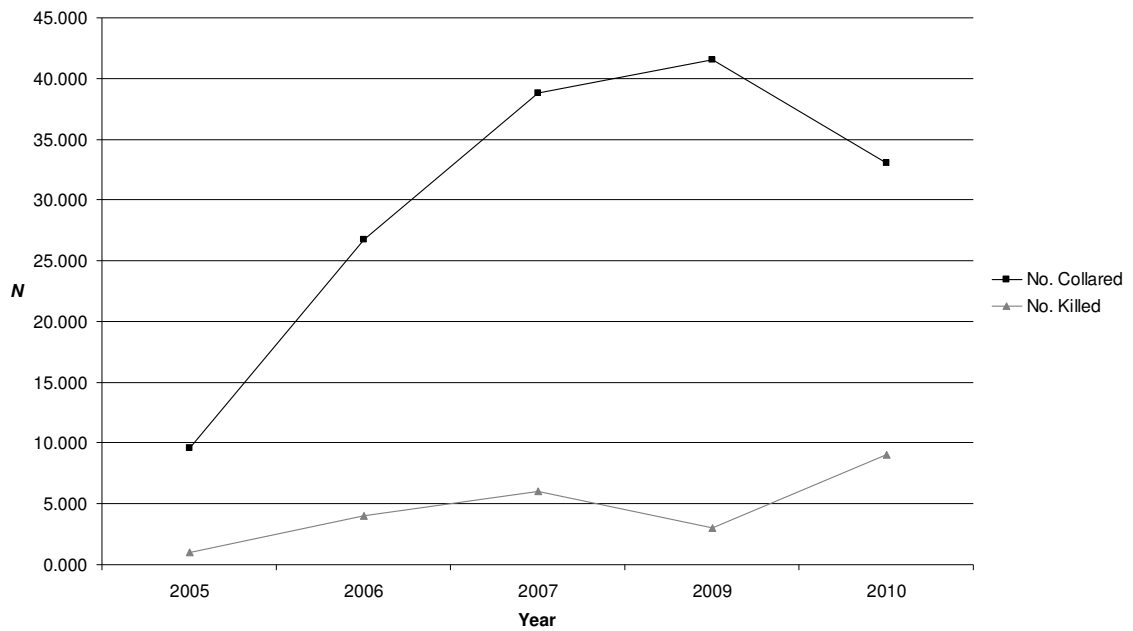


Figure 1.8. The number of mountain lions (*Puma concolor*) with functioning radiocollars present in the sampling area and the number of radiocollared mountain lions killed by hunters during the resampling period in the Black Hills, South Dakota.



CHAPTER 2: OCCURRENCES OF MOUNTAIN LIONS INVOLVED IN HUMAN- CONFLICTS

Abstract

In some states, mountain lion (*Puma concolor*) management has moved towards individual “problem” animal control, rather than population-level control. Summaries of lethal control data for livestock depredation and public safety identified subadult males as composing the largest proportion of animals that are lethally-removed. However, previous summaries implicating subadult males do not consider the composition of the population at-large and so managers are uncertain if subadult males make up the dominant numerical composition of both lethal removals and populations. Our objective was to compare composition of lethally-removed mountain lions and the mountain lion population at-large. We used mortality data collected by South Dakota Game, Fish, and Parks and composition of the population through our research activities throughout the Black Hills of South Dakota. We found that subadult males made up 33–41% of mountain lions that were lethally-removed in 3 of 4 years and 100% in 1 year. In comparison, subadult males made up only 9–17% (mean = 15%) of the population during the same years. In all 4 years of study, subadult males were lethally-removed more than expected based on their occurrence in the population. Conversely, adult females were lethally-removed less than expected during all 4 years of study. During all years combined, males of both age classes (e.g., subadult [1–3 yrs], adult [>3yrs]) were more often killed in livestock depredation incidents. Females (47%) comprised about half of the animals lethally-removed in public safety incidents and about 36% of incidents

involving domestic pets. The patterns of involvement in livestock depredation, public safety, and killing of domestic pets that we observed were similar to other studies and confirmed previous speculation that subadult males are more often involved in human-conflicts than expected based on population composition. We suggest that the intrinsic exploratory behavior most often exhibited by subadult males results in their encountering rural communities more frequently and their lower levels of hunting-experience and skill results in consumption of livestock and pets more often than other sex and age classes of mountain lion populations.

INTRODUCTION

Large carnivore management has changed from landscape-scale total population reduction to inclusion of prescriptions for identification and removal of offending individuals (Linnell et al. 1999, Anderson et al. 2010). Mountain lion (*Puma concolor*) management is controversial in the USA, with hunting for sport being the most controversial. Removal of mountain lions to protect native ungulates (e.g., bighorn sheep [*Ovis canadensis*]) and domestic livestock interests also is controversial and its efficacy has been questioned (Treves 2009). Government removal of mountain lions for public safety might be acceptable to the public, however, widespread population reduction to achieve the objective is not. To this end, efforts to identify and remove only so-called “problem” individuals have become common.

Male mountain lions are associated with livestock depredations more often than females (Aune 1991, Cunningham et al. 1995, Torres et al. 1996). Incidents involving domestic pets were slightly more often associated with female mountain lions (about 45%

male; Aune 1991, Beier 1991, Torres et al. 1996). However, Torres et al. (1996) pointed out that demographic data depicting the mountain lion population was lacking for their study, as was the case with previous studies (Beier 1991).

We investigated mountain lions removed via euthanasia by South Dakota Game, Fish and Parks for livestock depredation, public safety, and killing of domestic pets in relation to the simultaneous sample of radio-collared mountain lions within the same area to determine if various sex-age classes were involved in incidents more frequently than they occurred within the population. If the pattern observed by Aune (1991), Beier (1991), and Torres et al. (1996) is accurate, we would expect to find males more frequently involved in livestock depredation and females slightly more frequently involved in both public safety and domestic pet incidents and proportion of incidents attributed to sex-age classes would differ from the population at large.

STUDY AREA

We studied the mountain lion population occupying the Black Hills Ecoregion (N44.09375°, W103.77691°) between 2006 and 2009. The Black Hills occupy about 14,600 km² and are entirely surrounded by the Northern Great Plains. The Black Hills lie within South Dakota (~65%) and Wyoming (~35%), USA.

The Black Hills are an oblong-shaped complex of ridges, valleys, and steep canyons (Froiland 1990). Climate patterns in the Black Hills are characterized by hot summers and cold winters typical of a continental climate regime. The plant community is dominated by ponderosa pine (*Pinus ponderosa*) forests, but also contain spruce (*Picea glauca*), aspen (*Populus tremuloides*), and birch (*Betula* spp.) trees (Larson and Johnson

1999). Potential large prey species included white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), American bison (*Bison bison*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*) as well as many domestic livestock species. No other large carnivores were present in this system. Bobcat (*Lynx rufus*) and coyote (*Canis latrans*) are medium carnivores that occur sympatrically with mountain lions.

METHODS

Department Removals

We used the data set of mountain lions removed via euthanasia by South Dakota Department of Game, Fish, and Parks personnel from 1 January 2006 to 31 December 2009. Department officials aged and sexed each mountain lion using tooth eruption, tooth wear, and pelage characteristics (Anderson and Lindzey 2000), as well as an explanation of the reason for lethal removal. We reclassified removals based on department records as livestock depredation, domestic pets, within city limits, or proximity to houses. We pooled the categories “within city limits” and “proximity to houses” to reflect the ultimate reason as “public safety concerns.”

Radiocollared Sample

From 2006 – 2009, we conducted an ecological study of mountain lions, where we captured mountain lions and placed radiocollars on captured animals. We captured mountain lions >3 months old by using trained hounds (Hornocker 1970), foot-hold snares (Logan et al. 1999), foot-hold traps, wire-cage traps (Bauer et al. 2005), and free-dart (capture free-ranging animal by delivering immobilizing dart without prior restraint).

We immobilized animals by injecting captured animals with a mixture of telazol (tiletamine/zolazaline-hydrochloride, 4.84 mg/kg) and xylazine-hydrochloride (0.99 mg/kg, Kreeger 1996). We counteracted xylazine with yohimbine (0.125 mg/kg, Kreeger 1996). We aged captured animals by using tooth-eruption, tooth-wear, eye color, and pelage characteristics (Anderson and Lindzey 2000) and we classified animals as cub (≤ 1 yr), subadult (1–3 yrs), and adult (≥ 3 years). We placed MOD-500 (Telonics, Mesa, Arizona) radiocollars or global positioning system collars (single D-cell, Northstar Science and Technology, King George, Virginia) on animals >9 months of age and expandable MOD-125 (Telonics, Mesa, Arizona) radiocollars on cubs that were >3 weeks of age. Our capture and handling procedures followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the South Dakota State University Institutional Animal Care and Use Committee (Approval No. 07-A024).

For research captures, we attempted to capture animals in a random manner so as to ensure that the age structure of our radiocollared sample reflected the population composition. We used baited foot-snares year-long to capture mountain lions attempting to scavenge deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) carcasses without selecting for particular sex-age classes. We used hounds during winter; each day we released the hounds on the first track set that we encountered.

To reconstruct the population, we back-dated research-captured animals through time to reflect their known or probable existence within the population. Because of the differential immigration/emigration patterns in mountain lions (Sweaner et al. 2000, Thompson 2009), we back-dated all females until 1 year of age within the population and

back-dated adult males until 3 years of age. Subadult males were back-dated until 1 year of age only. For purposes of analysis, we considered the proportions of sex-age class composition at 1 January of each year to be reflective of the distribution of independent mountain lions throughout the year, when department removals were carried out.

Statistical Analysis

We compared department removals and the reconstructed population each year by using chi-squared tests for homogeneity. Sex-age class composition of department removals by year represent our observed values and annual population composition was used to calculate expected frequencies. For analyses where we differentiated among reasons for department removals, we compared the sum across years for sex-age classes to the means of yearly population composition. We used the sum of department removals by sex-age classes because each animal could only be sampled once (i.e., lethal removal), whereas we used the mean of yearly population composition because individual animals survived multiple years (Chapter 1). Thus, the mean estimated population composition 2006–2009 should reflect the total population from which animals could be involved in human conflicts throughout the duration of the study. We compared each type of incident (e.g., livestock depredation) with mean population composition using chi-squared tests for homogeneity, where sex-age classes by type of incident were our observed values and mean population composition frequencies were used to calculate expected frequencies.

RESULTS

South Dakota Game, Fish, and Parks lethally removed 41 mountain lions, 2006 – 2009 for reasons involving livestock depredation ($n = 11$), public safety ($n = 19$), and domestic pets ($n = 11$). Mean composition of department removals across years were 4.5 ± 0.87 (SE) subadult males, 1.75 ± 0.85 subadult females, 2.0 ± 1.08 adult males, and 2.0 ± 0.71 adult females per year, 2006–2009 (Table 2.1).

We continuously captured mountain lions from 1 January 2006 to 30 June 2009. Because we did not continuously capture animals after 30 June 2009, we used population composition data for the years 2006, 2007, 2008 to reflect the total population composition. Our estimate for population composition for 2009 was biased according to differential survival rates among sex-age classes in the population (Chapter 1). To compare department removals with population composition for 2009, we used the mean composition 2006–2009. Our population composition data was based on 108 (2006), 123 (2007), and 123 (2008) individual animals known to be alive in the study area during the study years (Table 2.2).

Mean population composition for 2006–2008 was 15% subadult male, 33% subadult female, 15% adult male, and 38% adult female (Table 2.3). Composition of department removals differed from the composition of the population at-large in 3 of 4 years (1-sided P -values range 0.003–0.01, Table 2.3). In all 4 years of study, subadult males were consistently removed more than they were present in the population at-large (1-sided P -values range 0.003 – 0.05). Mountain lions removed for depredating livestock were largely males of both age-classes; subadult females were notably absent (Table 2.3).

Subadult male mountain lions were removed for public safety reasons more often than expected (1-sided $P = 0.005$, Table 2.3). Subadult mountain lions of both sexes were the only animals removed for preying upon domestic pets and subadult males were removed more frequently than expected (1-sided $P < 0.0005$, Table 2.3).

DISCUSSION

Mountain lions are ubiquitous throughout the Black Hills Ecoregion and human residences are nearly so as well. We monitored numerous mountain lions during our overall research project and few occupied mountain lion home areas that did not contain any human residences (Chapter 4). Although, adult male mountain lions have larger home areas in the Black Hills than do other age and sexes of mountain lions, only few females occupy home areas that do not overlap with the distribution of domestic livestock. Thus, livestock distribution might not help explain differences observed. Subadult males are similar in physical size to adult females but are often heavier by the time they disperse (Jansen, B. D. and J. A. Jenks, South Dakota State University, *unpublished data*), which might not explain their higher involvement in depredation of livestock or pets. Generally speaking, we observed subadult male mountain lions traveling across the Black Hills during dispersal movements and thus, we would expect them to encounter human residences and cities more frequently than other sex-age classes. Notably, only subadults were removed in domestic pet incidents.

Of considerable note, none of the livestock depredation incidents involved domestic cattle, only 1 case involved domestic sheep, and 1 case involved a horse-colt, despite the year-round presence of cattle, sheep, and horses in the Black Hills, South

Dakota. Cunningham et al. (1995) found high levels of domestic cattle depredation, of which all were calves (<10 mths old). Fundamental differences in cattle husbandry likely explain the lack of cattle depredation in the Black Hills, where calves are born in late-winter (Mar–Apr) in sheds near residences; whereas in Arizona calving occurs on public rangelands. Instead of domestic cattle depredation, “hobby-livestock”, such as goats, llamas, miniature horses, and domesticated fowl (pea-fowl, geese) commonly made up livestock depredation cases in the Black Hills of South Dakota.

We observed a pattern of involvement in human-conflicts by subadult males that was remarkably similar to other regions (Aune 1991, Beier 1991, Torres et al. 1996). We found that subadult males are not only involved in more incidents than other sex-age classes, but they also are involved more often than they are represented in the population. Indeed, the pattern is clear that subadult males are more likely to be in conflict with humans than other sex-age classes. We hypothesize that the intrinsic exploring nature of subadult males and the lower hunting-experience level results in the observed patterns of sex-age class-specific involvement in human conflicts (Aune 1991, Beier 1991, Torres et al. 1996).

LITERATURE CITED

Anderson, C. R., Jr., and F. G. Lindzey. 2000. A guide to estimating mountain lion age classes. Wyoming Cooperative Fish and Wildlife Research Unit: Laramie, Wyoming, USA.

- Anderson, C. R., Jr., F. G. Lindzey, K. H. Knopff, M. G., Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America. Pages 41–54 *in* M. Hornocker and S. Negri, eds. *Cougar ecology and management*. The University of Chicago Press, Chicago, Illinois, USA.
- Aune, K. E. 1991. Increasing mountain lion populations and human-mountain lion interactions in Montana. Pages 86–94 *in* C. E. Braun, ed. *Mountain lion-human interaction symposium and workshop*. Colorado Division of Wildlife, Denver, Colorado, USA.
- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:446–471.
- Beier, P. 1991. Cougar attacks on humans in the United States and Canada, 1890–1990. *Wildlife Society Bulletin* 19:403–412.
- Cunningham, S. C., L. A. Haynes, C. Gustavson, and D. D. Haywood. 1995. Evaluation of the interaction between mountain lions and cattle in the Aravaipa-Klondyke area of southeast Arizona. *Arizona Game and Fish Department Research Branch Technical Report* 17:1–64.
- Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. Pages 191–207 *in* M. Festa-Bianchet and M. Apollonio, eds. *Animal behavior and wildlife conservation*. Island Press, Washington, DC, USA.

- Froiland, S. G. 1990. Natural history of the Black Hills and Badlands. The Center for Western Studies, Sioux Falls, South Dakota, USA.
- Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* 21: 1–39.
- Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. International Wildlife Veterinary Services. Laramie, Wyoming, USA.
- Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains: a field guide with color photographs. Fenske Media Corporation, Rapid City, SD, USA.
- Linnell, J. D., C. J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: Do “problem individuals” really exist? *Wildlife Society Bulletin* 27:698–705.
- Logan, K. A., L. L. Sweanor, J. F. Smith, and M. G. Hornocker. 1999. Capturing pumas with foot-hold snares. *Wildlife Society Bulletin* 27:201–208.
- Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798–808.

- Thompson, D. J. 2009. Population demographics of cougars in the Black Hills: survival, dispersal, morphometry, genetic structure, and associated interactions with density-dependence. Dissertation. South Dakota State University, Brookings, South Dakota, USA.
- Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. *Wildlife Society Bulletin* 24:451–460.
- Treves, A. 2009. Hunting for large carnivore conservation. *Journal of Applied Ecology* 46:1350–1356.

Table 2.1. Sex-age class composition and reason for mountain lions (*Puma concolor*) lethally removed from the Black Hills by South Dakota Game, Fish and Parks from 1 January 2006 to 30 December 2009. Sex of mountain lions are indicated as male (M) or female (F) and age-class as subadult (SA, 1–3 yrs old) and adult (A, >3 yrs old).

Type	Year	Total	Sex-Age Class			
			No. SM	No. SF	No. AM	No. AF
Dept. Removal	2006	12	4	4	1	3
Dept. Removal	2007	8	3	1	2	2
Dept. Removal	2008	4	4	0	0	0
Dept. Removal	2009	17	7	2	5	3
Dept. Removal	Mean (SE)	10.3 (2.8)	4.5 (0.9)	1.75 (0.9)	2.0 (1.1)	2.0 (0.7)
Livestock Dep.	All	11	5	0	5	1
Public Safety	All	19	8	5	2	4
Dom. Pets	All	11	7	4	0	0

Table 2.2. Composition of the mountain lion (*Puma concolor*) population occupying the Black Hills, South Dakota from captures during research activities and back-dated appropriately for respective sex-age classes, 2006–2009. Sex of mountain lions are indicated as male (M) or female (F) and age-class as subadult (S, 1–3 yrs old) and adult (A, >3 yrs old).

Year	Total	Age-class			
		No. SM	No. SF	No. AM	No. AF
2006	108	10	36	19	43
2007	123	20	41	16	46
2008	123	21	42	19	41
Mean (SE)	118 (5.0)	17.0 (2.5)	39.7 (1.3)	18.0 (0.7)	43.3 (1.0)

Table 2.3. Statistical analyses of the composition of mountain lions (*Puma concolor*) that were lethally removed by South Dakota Game, Fish, and Parks compared to the composition of the regional population, as measured by research captures from 2006–2009. Age class abbreviations are for subadult male (SM), subadult female (SF), adult male (AM), and adult female (AF).

Type	X^2 , d.f. = 3 (1-sided <i>P</i> -value)	Status	Age-class			
			SM	SF	AM	AF
Dept. 2006	14.05 (0.003)	Observed	4	4	1	3
Population 2006		Expected	1	2	4	5
Dept. 2007	6.66 (0.10)	Observed	3	1	2	2
Population 2007		Expected	1	3	1	3
Dept. 2008	12 (0.01)	Observed	4	0	0	0
Population 2008		Expected	1	1	0.1	1
Dept. 2009	10.82 (0.01)	Observed	7	2	5	3
Population mean (2006–2008)		Expected	3	6	3	6
Livestock	15.25 (0.003)	Observed	5	0	5	1
Population mean (2006–2008)		Expected	2	4	2	4
Public Safety	10.12 (0.02)	Observed	8	5	2	4
Population mean (2006–2008)		Expected	3	6	3	7
Domestic Pets	18.5 (<0.0005)	Observed	7	4	0	0
Population mean (2006–2008)		Expected	2	4	2	4

CHAPTER 3: DISEASE EXPOSURE IN MOUNTAIN LIONS

Abstract

The prevalence of select disease causing agents in mountain lions (*Puma concolor*) has been studied in extreme western and eastern (Florida) portions of the distribution of the species. Despite these accounts, little is known about infectious disease exposure in most of the geographic range. During other research on mountain lion ecology within the population occupying the Black Hills, South Dakota, we encountered numerous individuals showing emaciation, which resulted in concerns regarding potential presence of disease inducing agents. A battery of infectious agent assays were performed. We investigated the prevalence of disease-causing organisms on ocular swabs and in whole blood and serum samples from a total of 138 mountain lions sampled between 2006 and 2009 during research-related captures. The overall prevalence of potential ocular disease inducing agents was low with feline calicivirus (FCV) RNA being amplified most frequently from prevalent ocular swabs (4.7%). Of the blood borne agents, DNA of '*Candidatus Mycoplasma haemominutum*' was amplified most frequently (66%) whereas DNA of *M. haemofelis* was nearly absent (1%). Antibodies against feline/canine parvoviruses (F/CPV, 81%), *Toxoplasma gondii* (53%), FCV (27%), canine distemper virus (CDV, 18%), and feline immunodeficiency virus (13%) were commonly detected in serum the most prevalent disease-causing organisms in blood sera. While presence of nucleic acids of these agents or antibodies against the agents do not document clinical illness from infection, the results suggest that mountain

lions in the region are commonly exposed to a similar array of infectious agents known to cause illness in domestic cats.

INTRODUCTION

Disease prevalence in mountain lions is known only from California (Paul-Murphy et al. 1994), Florida (Roelke et al. 1993), Washington (Evermann et al. 1997), and parts of the northern Rocky Mountains (Biek et al. 2006). Yet, disease was the second leading cause of death in 2 studies of mountain lion ecology in North America (Beier and Barrett 1993, Logan and Sweanor 2001). Disease resulted in mortality in 17% of adult mountain lions in New Mexico (Logan and Sweanor 2001) and although, 3 of 27 (11%) cub mortalities were attributed to disease, 3 additional cubs died of “starvation” 1 week before the mother died of an undiagnosed disease. Mountain lion populations in the western USA do not appear to be threatened by catastrophic epizootics (Foley 1997), perhaps because most diseases do not affect mortality of adults or transmission rates are low due to low natural population densities. Nevertheless, it is important to understand the role of disease in the dynamics of mountain lion populations (e.g., Florida puma, Cunningham et al. 2008). Burgeoning human populations and associated pets (e.g., domestic cats) might play an increasing role in mountain lion population dynamics into the future.

In 2006, numerous mountain lions that were severely emaciated were incidentally captured as part of ongoing scientific research or euthanized by South Dakota Department of Game, Fish and Parks employees because of the poor condition and potential public safety concerns. There were also 2 animals with 1 or both eyes that

appeared cloudy and exhibited behavior suggesting the animals were blind. Lack of obvious factors causing emaciation and blindness led us to an investigation of the prevalence of diseases in the Black Hills mountain lion population. The isolated nature of this population and the density of human residents and recreational uses in the area, places increased importance on the understanding of all mortality factors, including diseases. Our specific objective was to investigate the prevalence of diseases in Black Hills mountain lions that are known to occur in other mountain lion populations or domestic cats.

STUDY AREA

We studied the mountain lion population occupying the Black Hills Ecoregion (N44.09375°, W103.77691°) between 2006 and 2009. Density of mountain lions on the study area was estimated to be about 2.0–2.5 independent animals per 100 km² (Chapter 1). The Black Hills occupy about 14,600 km² and are entirely surrounded by the Great Plains. The Black Hills are an oblong-shaped complex of ridges, valleys, and steep canyons (Froiland 1990). Climate patterns in the Black Hills are characterized by hot summers and cold winters typical of a continental climate regime. The plant community is dominated by ponderosa pine (*Pinus ponderosa*) forests, but also contain spruce (*Picea glauca*), aspen (*Populus tremuloides*), and birch (*Betula* spp.) trees (Larson and Johnson 1999). Potential large prey species included white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), American bison (*Bison bison*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*), as well as domestic livestock species. Relevant to disease

prevalence; domestic cats, coyotes (*Canis latrans*), bobcats (*Lynx rufus*) red foxes (*Vulpes vulpes*), skunks (*Mephitis* spp.), common raccoons (*Procyon lotor*), lagomorphs (*Sylvilagus* spp.), black-tailed prairie-dogs (*Cynomys ludovicianus*), red squirrels (*Tamiasciurus hudsonicus*), voles (*Microtus* spp.), and mice (*Peromyscus* spp.) were locally common and have all been found in diets of mountain lions in North America (Currier 1983).

METHODS

Field sampling

We captured mountain lions >3 months old by using trained dogs (Hornocker 1970), foot-hold snares (Logan et al. 1999), foot-hold traps, wire-cage traps (Bauer et al. 2005), and free-dart (capture free-ranging animal by delivering immobilizing dart without prior restraint). We immobilized captured animals by injecting captured animals with a mixture of telazol (tiletamine/zolazaline-hydrochloride, 5 mg/kg) and xylazine-hydrochloride (1 mg/kg, Kreeger 1996). We counteracted xylazine with yohimbine (0.125 mg/kg, Kreeger 1996). Our capture and handling procedures followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the South Dakota State University Institutional Animal Care and Use Committee (Approval No. 07-A024).

We aged captured animals by using tooth-eruption, tooth-wear, eye color, and pelage characteristics (Currier 1983, Anderson and Lindzey 2000) and we classified animals as cub (≤ 1 yr), subadult (1–3 yrs), and adult (≥ 3 years). To investigate ocular diseases, we took 2 ocular swab samples (BBL Culture Swab, BD, Franklin Lakes, NJ)

from underneath upper, lower, and third eyelids of each eye, placed the samples in transportation tubes, and stored swab samples in a freezer at -40° C. We withdrew 12 ml of whole blood, by venipuncture of the medial saphenous or cephalic vein. While in the field, we placed 3 ml of whole blood in a storage tube containing an anti-coagulant (EDTA, Tyco Healthcare Group LP, Mansfield, MA) for testing and 9 ml in serum separation tubes (SST, BD, Franklin Lakes, NJ) and used ice coolers to maintain cool-storage conditions in summer and prevent freezing in cold ambient temperatures in winter. After 4 hrs elapsed since withdrawing blood, we used a centrifuge to separate serum and stored serum and whole blood at -40° C until tested.

Laboratory testing

Aliquots of the samples were shipped to the Center for Companion Animal Studies in the Department of Clinical Sciences at Colorado State University by overnight express on ice. Samples were either processed on arrival or were frozen at - 80°C until assayed. Total DNA and RNA were extracted from whole blood and ocular swabs and evaluated for selected pathogens. Molecular assays for amplification of DNA of feline herpesvirus 1 (FHV-1), DNA of *Mycoplasma* spp., DNA of *Chlamydomphila felis*, and RNA of feline calicivirus (FCV) were performed on ocular samples (Low et al. 2007). Total DNA extracted from blood was evaluated in a PCR assay that amplifies the DNA of haemotropic mycoplasmas (Jensen et al. 2001); an assay that amplifies the DNA of *Ehrlichia* spp., *Anaplasma* spp., *Neorickettsia* spp., *Wolbachia* spp. (Lappin et al. 2004); and an assay that amplifies the DNA of *Bartonella* spp. (Jensen et al. 2000). Samples positive for DNA of the *Ehrlichia/Anaplasma/Neorickettsia/Wolbachia* group, DNA of

M. haemofelis, or DNA of *Bartonella* spp. were evaluated by genetic sequencing to further determine the infective species using a commercially available service (Macromolecular Resources, Colorado State University, Fort Collins, CO).

Serum antibodies against feline leukemia virus and feline immunodeficiency virus were measured by use of a commercially available kit marketed for use with samples from domestic cats (SNAP® FeLV/FIV, Idexx Laboratories, Portland ME) following the manufacturer's instructions. Serum antibodies against *Toxoplasma gondii* and *Bartonella* spp. were measured by previously reported microELISA (Vollaire et al. 2005, Lappin et al. 2009). Serum neutralization assays were used to detect antibodies against FCV, FHV-1, and canine distemper virus. Antibodies against canine or feline parvoviruses were measured by hemagglutination inhibition; however, whether the antibodies were induced by exposure to dog or cat strains could not be determined. The serum neutralization and hemagglutination inhibition assays were performed by the Veterinary Diagnostic Laboratory at Colorado State University. This laboratory is accredited (full service, all species) by the American Association of Veterinary Laboratory Diagnosticians (AAVLD) meeting standards based on ISO17025 / OIE (<http://dlab.colostate.edu/>) and is also a member of the National Animal Health Laboratory Network (NAHLN). Antibodies against plague (*Yersinia pestis*) were measured by an agglutination assay performed by the Centers for Disease Control in Fort Collins, Colorado.

Analysis

Because family member exposure to diseases might not be independent from other animals, when we captured family members, we report the results of the mother or

1 sibling (absence of mother) with cumulative disease exposures (e.g., sibling A exposed to disease X and sibling B exposed to disease Y equals 1 animal exposed to diseases X and Y). We also recaptured animals several times, in these cases we report cumulative exposure; to account for organisms detected in different samples. Not all individuals were tested for all diseases.

Statistics – We tested for differences between male and female exposure rates by using Fisher’s Exact Test for each disease organism. For each disease with ≥ 10 positive cases, we tested for differences between subadults and adult by sex.

RESULTS

We sampled 138 individual mountain lions 157 times, 2006–2009. Of these 138 individuals, 97 were independent from other sampled animals (not family members).

Ocular swabs

Few animals tested positive for exposure to organisms found in ocular samples (Table 3.1). No animals tested positive for *Chlamydia felis*. We found no differences in exposure rates to FHV ($P \leq 1.00$), *Mycoplasma* spp. (2-sided $P \leq 1.00$), or FCV (2-sided $P \leq 1.00$) in ocular samples of male and female animals.

Whole blood

In samples of whole blood from males and females combined, we consistently detected *Mycoplasma haemominutum* ($n_{\text{positive}} = 64$) and rarely detected *Ehrlichia* spp. ($n_{\text{positive}} = 3$), *Mycoplasma haemofelis* ($n_{\text{positive}} = 1$), and *Bartonella* spp. ($n_{\text{positive}} = 2$; Table 3.2). We found similar exposure rates to *Ehrlichia* spp. (2-sided $P = 0.56$), *Mycoplasma haemofelis* (2-sided $P = 1.00$), or *Bartonella* spp. (2-sided $P = 0.51$) for

males and females. Adult females tested positive for *Mycoplasma haemominutum* in whole blood samples more frequently than adult males (2-sided $P = 0.05$). Subadult ($n = 9$) and adult ($n = 47$) females had similar exposure rates (2-sided $P = 0.42$), whereas adult males ($n = 18$) tested positive more frequently than subadult males ($n = 16$, 2-sided $P = 0.001$).

Blood sera

In sera, no animals tested positive for *Toxoplasma* IgM. We found 52.6% of samples tested positive for exposure to *Toxoplasma* IgG and 7.2% were positive for *Bartonella* IgG (Table 3.3). There were no differences in exposure rates of male and female animals to *Toxoplasma* IgG (2-sided $P = 0.31$) or *Bartonella* IgG (2-sided $P = 0.43$). There were no age-class differences in exposure rates to *Toxoplasma* IgG among females ($n = 9$ subadult F, $n = 47$ adult F; 2-sided $P = 0.15$) or males ($n = 16$ subadult M, $n = 18$ adult M; 2-sided $P = 0.33$).

We found frequent exposure to some viruses found in other populations (Table 3.4). No animals tested positive for exposure to plague. There were no differences between male and female exposure rates to viruses (FIV, 2-sided $P = 0.76$; FLV, 2-sided $P = 0.41$; FHV, 2-sided $P = 0.42$; FCV, 2-sided $P = 0.46$; F/CPV, 2-sided $P = 0.27$; CDV, 2-sided $P = 0.78$). Among females, there were no age class-differences in exposure rates to most viruses (FIV, 2-sided $P = 0.58$; FCV, 2-sided $P = 0.24$; CDV, 2-sided $P = 0.58$); however, adult females had higher exposure rates than subadult females to F/CPV (2-sided $P = 0.003$). Among males, there were no age class-differences in exposure rates to most viruses (FIV, 2-sided $P = 0.11$; FCV, 2-sided $P = 0.69$; F/CPV, 2-sided $P = 0.17$);

however, adult males had higher exposure rates than subadult males to CDV (2-sided $P = 0.007$).

DISCUSSION

Disease was a potential cause of death in 16% of subadult (1–3 yrs old) and adult (>3 yrs) mountain lion mortalities and 10% in cubs (<1 yr) that we investigated during our research (Chapter 1). Because of the difficulty in detecting a death and prompt laboratory examination during field research, we were unable to conclusively determine causative agents for those cases. However, our findings reported here implicate some organisms over others.

Ocular disease

This study is the first to routinely sample mountain lions for ocular disease-causing organisms. We found low prevalences and our results could be used as references for others populations. Of note, we found 1 and 4 cases of apparently acute and chronic disease resulting in corneal opacity due to neutrophil infiltration of the corneal tissues. Diagnoses were keratitis (1 acute case) and uveitis (1 chronic case). Causative agents of these cases have not been determined and investigation has been hindered by the low occurrence of clinically-affected animals exhibiting active disease.

Whole blood

The epidemiology of *Mycoplasma* is poorly understood (Criado-Fornelio et al. 2003). *Mycoplasma haemominutum* can cause anorexia, depression, weakness, and weight loss during acute disease (Schoeman et al. 2001). Adult males had the highest

exposure rates compared to other sex-age classes, which suggests they have higher social contact rates.

Sera

Toxoplasma

Toxoplasma gondii was detected in 53% of sampled mountain lions in our study, which was similar to California mountain lions (Paul-Murphy et al. 1994). Roelke et al. (1993) found only 9% exposure and suggested that the test they used might be insufficient to detect *T. gondii*. *Toxoplasma gondii* causes clinical symptoms of diarrhea, pneumonia, ocular disease, and abortion (Frenkel et al. 1987). Prevalence of *T. gondii* was high in adult females (62%), but the role this organism might play in cub mortality requires more research.

Feline immunodeficiency virus

Domestic cats in North America that are allowed to roam outside exhibit seroprevalence of FIV in about 4% of animals tested (Levy et al. 2006). Overall prevalence in mountain lions from our study (12%) was much higher than reported for domestic cats (4%). Mountain lions in California had 0% prevalence for FIV (Paul-Murphy 1994), whereas in Florida, Wyoming/Montana, and Washington prevalence was much higher (37%, Roelke et al. 1993; 19–50%, Biek et al. 2006; 25%, Evermann et al. 1997). In our study, animals that subsequently tested positive for FIV (22%) did not show clinical symptoms of disease. The lack of clinical symptoms in the animals that tested positive might be a reflection of the evolutionary history of FIV and mountain lions (Carpenter et al. 1996).

Feline calicivirus

Feline calicivirus was the second most common virus found in our study. Exposure rates for Black Hills mountain lions were similar to mountain lion populations elsewhere (Roelke et al. 1993, Paul-Murphy et al. 1994, Biek et al. 2006). Feline calicivirus is the primary agent causing respiratory disease and, although not fatal in adults, FCV can be fatal in cubs (<10 wks old). Because FCV can be fatal in young cubs, we suggest future research should test mothers and cubs for the disease while cubs are still in natal dens.

Feline/canine parvovirus

Feline/canine parvovirus can cause mortality especially in young animals (Scott 1990). Exposure rates for F/CPV (81%) in mountain lions in the Black Hills were similar to those reported elsewhere (58–100%, Roelke et al. 1993, Paul-Murphy et al. 1994, Biek et al. 2006). Disease was implicated in 10% of cub mortalities, which might be related to high prevalences of F/CPV in adult mountain lions. We sampled blood from cubs >4 months old and found 31% positive for F/CPV. These animals already survived the early mortality period (Chapter 1 and Logan and Sweanor 2001) and thus, might not be useful in determining the role F/CPV plays in cub survival. Although we routinely captured cubs 2–4 weeks old, withdrawing blood for disease testing was not performed. Clearly future research in cub survival should attempt to include disease testing beginning with first capture in natal dens, while most cubs are still alive.

Canine distemper virus

Canine distemper virus is present in many carnivore species (Munson 2001) and Biek et al. (2006) suggested that CDV persists in carnivores other than mountain lions. Evidence of their conclusion was the sporadic prevalence among years within populations they studied. We found positive status in 18% of all mountain lions, which was similar to the highest prevalences reported for Wyoming (Biek et al. 2006). Our study duration was 3 years and positive cases were only found in the last 2 years (2007–2009) of the study, despite 36% of samples coming from mountain lions in 2006. We suggest that our study coincided with a period of increasing incidence of CDV, similar to that reported by Biek et al. (2006).

Plague

We did not detect prior exposure to plague in any mountain lions that were sampled. Although thought to be especially pathogenic in felids (Thorne et al. 1982, cited in Logan and Sweanor 2001), 44% of domestic cats orally-infected became ill and recovered (Perry and Fetherston 1997). Our study was 3 years in length and Biek et al. (2006) reported finding plague exposures sporadically by population within Wyoming and between years within populations. Plague was also a relatively new disease in South Dakota and had not been detected prior to 1994 (Perry and Fetherston 1997). Additionally, plague exposure by mountain lions is thought to be most prevalent at low primary prey abundances, when mountain lions are more likely consuming higher numbers of alternate prey, including rodents and lagomorphs (Logan and Sweanor 2001). There were 3 deer species (white-tailed deer, mule deer, and elk) in high abundance in

the Black Hills, as well as pronghorn, bison, mountain goats, and bighorn sheep; thus mountain lions might not have utilized plague-prone species (e.g., prairie-dogs [*Cynomys ludovicianus*], squirrels [*Sciurus* spp., *Tamiasciurus hudsonicus*], during this study.

Biologists investigating dead mountain lions that appear physically normal and no field evidence is suggestive of a traumatic-cause of death, should be wary of the potential for plague-induced mortality. Especially, if illness occurs within several days, as one biologist perished from plague in 2007, after performing a necropsy on a dead mountain lion in Arizona.

Future disease research

There remains a need to further identify the role of disease in mountain lion population dynamics, especially in neonatal cubs. This could be easily addressed by using adult females with radiocollars. Adult females with radiocollars provide the location of den-sites with neonatal cubs. The behavior of adult females remaining within the den, even during close approach by researchers (Sweaner et al. 2005) can be exploited to simultaneously capture neonatal cubs and the adult female. When necessary, we were successful in free-darting adult female mountain lions within den-sites. We used 2 persons; 1 person provided visual distraction while another person fired a dart through small openings in vegetation and boulders, into large muscle masses of the female. We recorded no negative influences on cub survival and no accidents occurred during these operations. If desired, the adult female could be captured with traps near the den-site, by placing food-baited traps or traps with an auditory sounds as bait. During capture, both mother and cubs might be sampled for diseases and radiocollared. Radiocollars provide

the opportunity to investigate future mortality as well as recapture animals with high titers to elucidate the possibility of recovery, increasing, or persistent infection.

LITERATURE CITED

- Anderson, C. R., Jr., and F. G. Lindzey. 2000. A guide to estimating mountain lion age classes. Wyoming Cooperative Fish and Wildlife Research Unit: Laramie, Wyoming, USA.
- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:446–471.
- Beier, P., and R. H. Barrett. 1993. The cougar in the Santa Ana Mountain Range, California. Final Report, Orange City Mountain Lion Study. University of California, Berkeley.
- Biek, R., T. K. Ruth, K. M. Murphy, C. R. Anderson, Jr., M. Johnson, R. DeSimone, R. Gray, M. G. Hornocker, C. M. Gillin, and M. Poss. 2006. Factors associated with pathogen seroprevalence and infection in Rocky Mountain cougars. *Journal of Wildlife Diseases* 42:606–615.
- Carpenter, M. A., E. W. Brown, M. Culver, W. E. Johnson, J. Pecon-Slattery, D. Brousset, and S. J. O'Brien. 1996. Genetic and phylogenetic divergence of feline immunodeficiency virus in the puma (*Puma concolor*). *Journal of Virology* 70:6682–6693.

- Criado-Fornelio, A., A. Martinez-Marcos, A. Buling-Sarana, J. C., Barba-Carretero. 2003. Presence of *Mycoplasma haemofelis*, *Mycoplasma haemominutum*, and piroplasmids in cats from southern Europe: a molecular study. *Veterinary Microbiology* 93:307–317.
- Cunningham, M. W., M. A. Brown, D. B. Shindle, S. P. Terrell, K. A. Hayes, B. C. Ferree, R. T. McBride, E. M. Blankenship, D. Jansen, S. B. Citino, M. E. Roelke, R. A. Kiltie, J. L. Troyer, and S. J. O'Brien. 2008. Epizootiology and management of feline leukemia virus in the Florida puma. *Journal of Wildlife Diseases* 44:537–552.
- Currier, M. J. P. 1983. *Felis concolor*. *Mammalian Species* 200:1–7.
- Evermann, J. F., W. J. Foreyt, B. Hall, and A. J. McKeirnan. 1997. Occurrence of puma lentivirus infection in cougars from Washington. *Journal of Wildlife Diseases* 33:316–320.
- Foley, J. E. 1997. The potential for catastrophic infectious disease outbreaks in populations of mountain lions in the western United States. Pages 29–36 in W. D. Padley, ed. *Proceedings of the 5th Mountain Lion Workshop*. San Diego, CA.
- Frenkel, J. K., A. B. Keir, J. E. Wagner, and J. Holzworth. 1987. Protozoan diseases. Pages 359–405 in J. Holzworth, ed. *Diseases of the cat: medicine and surgery*. W. B. Saunders, Philadelphia, Pennsylvania, USA.
- Froiland, S. G. 1990. *Natural history of the Black Hills and Badlands*. The Center for Western Studies, Sioux Falls, South Dakota, USA.

- Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* 21:1–39.
- Jensen, W. A., M. Z. Fall, J. Rooney, D. L. Kordick, and E. B. Breitschwerdt. 2000. Rapid identification and differentiation of *Bartonella* species using a single-step PCR assay. *Journal of Clinical Microbiology* 38:1717–1722.
- Jensen, W. A., M. R. Lappin, S. Kamkar, and W. Reagan. 2001. Use of a polymerase chain reaction assay to detect and differentiate two strains of *Haemobartonella felis* in naturally infected cats. *American Journal of Veterinary Research* 62:604–608.
- Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. International Wildlife Veterinary Services. Laramie, Wyoming, USA.
- Lappin M. R., E. B. Breitschwerdt, M. Brewer, J. R. Hawley, and B. Hegarty. 2009. Prevalence of *Bartonella* species DNA in the blood of cats with and without fever. *Journal of Feline Medicine and Surgery* 11:141–148.
- Lappin M. R., E. B. Breitschwerdt, W. A. Jensen, et al. 2004. Molecular and serological evidence of *Anaplasma phagocytophilum* infection of cats in North America. *Journal American Veterinary Medical Association* 225:893–896.

- Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains: a field guide with color photographs. Fenske Media Corporation, Rapid City, SD, USA.
- Levy, J. K., H. M. Scott, J. L. Lachtara, and P. C. Crawford. Seroprevalence of feline leukemia virus and feline immunodeficiency virus infection among cats in North America and risk factors for seropositivity. 2006. *Journal of the American Veterinary Medical Association* 228:371–376.
- Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology of an enduring carnivore. Island Press, Washington, DC, USA.
- Logan, K. A., L. L. Sweanor, J. F. Smith, and M. G. Hornocker. 1999. Capturing pumas with foot-hold snares. *Wildlife Society Bulletin* 27:201–208.
- Low, H. C., C. C. Powell, J. K. Veir, J. R. Hawley, and M. R. Lappin. 2007. Prevalence of feline herpesvirus 1, *Chlamydomphila felis*, and *Mycoplasma* spp DNA in conjunctival cells collected from cats with and without conjunctivitis. *American Journal of Veterinary Research* 68:643–648.
- Munson, L. 2001. Feline morbillivirus infection. Pages 59–62 in E. S. Williams and I. K. Barker, eds. Iowa State University Press, Ames, Iowa, USA.
- Paul-Murphy, J., T. Work, D. Hunter, E. McFie, and D. Fjelline. 1994. Serologic survey and serum biochemical reference ranges for free-ranging mountain lion (*Felis concolor*) in California. *Journal of Wildlife Diseases* 30:305–315.
- Perry, R. D., and J. D. Fetherston. 1997. *Yersinia pestis*—Etiologic agent of plague. *Clinical Microbiology Reviews* 10:35–66.

- Roelke, M. E., D. J. Forrester, E. R. Jacobson, G. V. Kollias, F. W. Scott, M. C. Barr, J. F. Evermann, and E. C. Pirtle. 1993. Seroprevalence of infectious disease agents in free-ranging Florida panthers (*Felis concolor coryi*). *Journal of Wildlife Diseases* 29:36–49.
- Schoeman, T. R. G. Lobetti, L. Jacobson, and B. Penzhorn. 2001. Feline babesiosis: signalment, clinical pathology, and concurrent infections. *Journal of South African Veterinary Association* 81:73–78.
- Sweaner, L. L. K. A. Logan, and M. G. Hornocker. 2005. Puma responses to close approaches by researchers. *Wildlife Society Bulletin* 33:905–913.
- Vollaire, M. R., S. V. Radecki, and M. R. Lappin. 2005. Seroprevalence of *Toxoplasma gondii* antibodies in clinically ill cats of the United States. *American Journal of Veterinary Research* 66:874–877.

Table 3.1. Exposure frequencies and sample sizes of disease-causing organisms in ocular swab samples from both eyes of mountain lions (*Puma concolor*) sampled in the Black Hills, South Dakota, 2006–2009. Sex represented as F (female), M (male), All (both sexes).

Sex	% Positive ($n_{\text{positive}}/n_{\text{total}}$)			
	Fel. Herpes Virus	<i>Mycoplasma</i> spp.	<i>Chlamydophila felis</i>	Fel. Calici Virus
F	1.8 (1/57)	1.8 (1/55)	0.0 (0/55)	5.5 (3/55)
M	2.6 (1/38)	0.0 (0/30)	0.0 (0/30)	3.3 (1/30)
Both	2.1 (2/95)	1.2 (1/85)	0.0 (0/85)	4.7 (4/85)

Table 3.2. Exposure frequencies and sample sizes for disease-causing organisms in whole blood samples from mountain lions (*Puma concolor*) in the Black Hills, South Dakota 2006–2009. Sex represented as F (female), M (male), All (both sexes). Age represented by SA (subadult, 1–3 yrs old), A (adult, >3 yrs old), All (both ages combined).

Sex	Age	% Positive ($n_{\text{positive}}/n_{\text{total}}$)			
		<i>Erhlichia</i> spp.	<i>Mycoplasma</i> <i>haemofelis</i>	<i>Mycoplasma</i> <i>haemominutum</i>	<i>Bartonella</i> spp.
F	SA			66.7 (6/9)	
F	A			78.7 (37/47)	
F	All*	1.7 (1/58)	1.7 (1/58)	74.1 (43/58)	3.4 (2/58)
M	SA			31.3 (5/16)	
M	A			88.9 (16/18)	
M	All*	5.1 (2/39)	0.0 (0/39)	53.8 (21/39)	0.0 (0/39)
All	All*	3.1 (3/97)	1.0 (1/97)	66.0 (64/97)	2.1 (2/97)

* includes small number of cubs (<1 yr old)

Table 3.3. Exposure frequencies and sample sizes for disease-causing organisms in blood sera of mountain lions (*Puma concolor*) sampled in the Black Hills, South Dakota, 2006–2009. Sex represented as F (female), M (male), All (both sexes). Age represented by SA (subadult, 1–3 yrs old), A (adult, >3 yrs old), All (both ages combined).

Sex	Age	% Positive ($n_{\text{positive}}/n_{\text{total}}$)		
		<i>Toxoplasma</i> IgM	<i>Toxoplasma</i> IgG	<i>Bartonella</i> IgG
F	SA		33.3 (3/9)	
F	A		61.7 (29/47)	
F	All*	0.0 (0/58)	56.9 (33/58)	5.2 (3/58)
M	SA		37.5 (6/16)	
M	A		55.6 (10/18)	
M	All*	0.0 (0/39)	46.2 (18/39)	10.3 (4/39)
All	All*	0.0 (0/97)	52.6 (51/97)	7.2 (7/97)

* includes small number of cubs (<1 yr old)

Table 3.4. Exposure frequencies for select disease-causing virus in blood sera of mountain lions (*Puma concolor*), Black Hills, South Dakota, 2006–2009. Sex represented as F (female), M (male), All (both sexes). Age represented by SA (subadult, 1–3 yrs old), A (adult, >3 yrs old), All (both ages combined). Viruses listed as FIV (feline immunodeficiency virus), FLV (feline leukemia virus), FHV (feline herpes virus), FCV (feline calici virus), F/CPV (feline/canine non-specific parvo virus), CDV (canine distemper virus), Plague (*Yersinia pestis*).

Sex	Age	% Positive ($n_{\text{positive}}/n_{\text{total}}$)						
		FIV	FLV	FHV	FCV	F/CPV	CDV	Plague
F	SA	0 (0/9)			11.1 (1/9)	55.6 (5/9)	0 (0/9)	
F	A	15.2 (7/46)			34.2 (13/38)	97.4 (37/38)	15.8 (6/38)	
F	All*	14.0 (8/57)	0.0 (0/57)	0.0 (0/49)	30.6 (15/49)	85.7 (42/49)	16.3 (8/49)	0.0 (0/36)
M	SA	0 (0/16)			26.7 (4/15)	73.3 (11/15)	0 (0/15)	
M	A	22.2 (4/18)			18.8 (3/16)	93.8 (15/16)	43.8 (7/16)	
M	All*	10.3 (4/39)	2.6 (1/39)	2.8 (1/36)	22.2 (8/36)	75.0 (27/36)	19.4 (7/36)	0.0 (0/32)
All	All*	12.5 (12/96)	1.0 (1/96)	1.2 (1/85)	27.1 (23/85)	81.2 (69/85)	17.6 (15/85)	0.0 (0/68)

* includes small number of cubs (<1 yr old)

CHAPTER 4. HUMAN-HOUSING AND MOUNTAIN LIONS:
INFLUENCE ON SURVIVAL AND DISEASE EXPOSURE

Abstract

Human occupancy and development is an increasing conservation concern worldwide. Contrary to past habitation patterns in the United States, recent trends show increased movement away from city centers and increased habitation in rural areas. Human residences are ubiquitous throughout the Black Hills, South Dakota and might represent a foreshadowing of future settlement in currently undeveloped areas of the western United States. We investigated the relationship between proportion of mountain lion (*Puma concolor*) home areas ≤ 200 m from a residence and adult survival and disease exposure. We used program MARK to estimate survival rates with proportion of home area ≤ 200 m from a residence and sex as covariates. We used logistic regression with exposure to specific diseases as the response and proportion of home area ≤ 200 m from a residence and sex as covariates. We found animals with a range of 0–33% of their home area ≤ 200 m from a residence. We found an inverse relationship between increasing area ≤ 200 m from a residence and adult survival of mountain lions. We found that adult male survival of mountain lions was more sensitive to human residences than adult females. Survival rates declined below 0.80 for adult males and female mountain lions when proportion of home areas ≤ 200 m from a residence reached 40% and 60%, respectively. We found no relationship between residences and disease exposure for adult male or female mountain lions. We suggest that our sample of mountain lions with 0 residences within their home areas ($n = 3$) was too low to adequately understand disease exposure in

areas void of human residences. Mountain lions appear to be sensitive to exurban-type development and landscape managers will be instrumental in shaping the fauna of areas via decisions made regarding development.

INTRODUCTION

Human development of wild areas is proceeding at a high rate. Land conversion from natural areas to residential areas has been highest in the western United States (Baron et al. 2000). In recent decades, residential movement from large urban centers into natural areas has increased with exurban development (Theobald 2003). Exurban developments are areas with low-density residential housing (6-12 houses/km² or 1 house/5–40 acres) that are not contiguous with urban areas. In comparison, suburban development is characterized as higher density housing that borders urban development on at least one side. Despite low density housing in exurban areas, recent research has demonstrated negative effects on biodiversity and on some taxonomic groups or individual species. Generally speaking, species sensitive to disturbances, interior patch species, or those with habitat preferences for dense shrub or tall grass vegetation decline with exurban development and those that are human commensal, agricultural, or generalists increase and spread along with residential development (Odell and Knight 2001, Maestas et al. 2003).

Mountain lions (*Puma concolor*) are a habitat and dietary generalist that might be capable of establishing in suburban and exurban areas (Burdett et al. 2010). However, human intolerance prevents persistence of mountain lions in conjunction with suburban areas. Mountain lions do use suburban and exurban areas, evidenced by numerous

photographs circulating on the internet or by recent research using global positioning system (GPS) collars on mountain lions (Kertzen 2008, Burdett et al. 2010). In California, mountain lions used exurban development (6 houses/km² or 1 house/40 acres) less than expected within their home areas (Orlando 2008, Burdett et al. 2010). Overall survival was lower in areas of increased human development (Orlando 2008) and animals that exhibited a neutral response to exurban developments had lower survival than animals that avoided exurban areas (Burdett et al. 2010). Research in areas outside of California has documented similar patterns of avoidance (Mattson et al. 2007, Nicholson 2009).

Diseases of mountain lions can co-occur in populations of domestic cats (Roelke et al. 1993, Paul-Murphy et al. 1994). Some disease (e.g., parvo virus) might be endemic within mountain lion populations (Biek et al. 2006); whereas domestic cats might be reservoirs for disease persistence. Thus, mountain lions living in areas with higher populations of domestic cats might be more frequently exposed than mountain lions occupying large areas void of human residences. Because mountain lions interact directly (i.e., predation) or indirectly (i.e., scent left at scrape sites or feces) with domestic cats, disease transmission is possible in areas surrounding human residences.

Our objectives were to investigate the role of human housing in survival and disease exposure among mountain lions in a relatively rural landscape. The landscape to some degree contrasts with many western United States landscapes. Currently, the western United States is developed in a clustered pattern, where large areas are void of residential housing and exurban developments are closer to areas of higher density

development. This pattern has occurred because of government encouragement and pioneering land settlement in centuries past. However, land use conversion from ranching, typical of pioneering land settlement patterns, to exurban development is driven by increased interest in “rural” lifestyles.

The Black Hills of South Dakota contrast with many current landscapes of the western United States; human residential occupancy is ubiquitous throughout. Historic patterns of mountain lion occupancy differ as well. Mountain lions were reduced but not extirpated from the mountainous areas of the western United States and have relatively recently experienced residential development in previously natural landscapes. However, large areas remain void of human residences. In contrast, mountain lions were extirpated, or nearly so, from the Black Hills in the early 1900s. However, later in the 1900s, mountain lions recolonized an already human dominated landscape (Thompson 2009). Thus, mountain lions maintain home areas in a continuum of human residences, from none to high residential density typical of incorporated cities. To some degree, if development patterns continue unabated, the residential development of the Black Hills provides a foreshadowing of future development patterns in larger areas of the western United States. An understanding of the relationship between human occupancy and mountain lion survival and disease exposure would increase society’s ability to maintain mountain lion populations.

STUDY AREA

We studied the mountain lion population occupying the Black Hills Ecoregion (N44.09375°, W103.77691°) between 2006 and 2009. The Black Hills occupy about

14,600 km² and are entirely surrounded by the Northern Great Plains. The Black Hills lie within South Dakota (~65%) and Wyoming (~35%), USA.

The Black Hills are an oblong-shaped complex of ridges, valleys, and steep canyons (Froiland 1990). Highest elevations (ca. 2,100 m) occur in the west-central area and surface water drainages radiate outward in all directions (Froiland 1990). Climate patterns in the Black Hills are characterized by hot summers and cold winters typical of a continental climate regime. The plant community is dominated by ponderosa pine (*Pinus ponderosa*) forests, but also contains spruce (*Picea glauca*), aspen (*Populus tremuloides*), and birch (*Betula* spp.) trees (Larson and Johnson 1999). Potential large prey species included white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), American bison (*Bison bison*), mountain goat (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*) as well as many domestic livestock species. No other large carnivores were present in this system. Bobcat (*Lynx rufus*) and coyote (*Canis latrans*) are medium carnivores that occur sympatrically with mountain lions.

Private in-holdings within the Black Hills National Forest (United States Forest Service) and human residences are ubiquitous throughout the area. There are 8 small cities within the Black Hills and 8 small and large (>8,600 people, United States Census Bureau 2000) cities along the perimeter of the Black Hills that are within or border mountain lion habitat (Table 4.1). There are numerous exurban developments within the Black Hills and many more individual residences. Generally, 9.2% of the Black Hills in South Dakota was $\leq 200\text{m}$ from a residence. On average, there were 7.14 residences/km² in our study area. Mountain lion density in our study area averaged 2.43/100 km² for

independent animals (subadult [1–3 yrs] + adult) and ranged from 2.0–2.5, 2006–2010 (Chapter 1).

METHODS

Captures

We captured mountain lions by using trained dogs (Hornocker 1970), foot-hold snares (Logan et al. 1999), foot-hold traps, wire-cage traps (Bauer et al. 2005), and free-dart (capture free-ranging animal by delivering immobilizing dart without prior restraint). We immobilized animals by injection with a mixture of telazol (tiletamine/zolazaline-hydrochloride, 4.84 mg/kg) and xylazine-hydrochloride (0.99 mg/kg, Kreeger 1996). We counteracted xylazine with yohimbine (0.125 mg/kg, Kreeger 1996). We aged captured animals by using tooth-eruption, tooth-wear, and pelage characteristics (Anderson and Lindzey 2000). We classified animals as cubs (<1 yr), subadults (1–3 yrs), and adults (≥ 3 years). We placed radiocollars (MOD-500, Telonics, Mesa, Arizona) and eartags (Allflex, Dallas, Texas, USA) on each mountain lion. During each capture, we withdrew 12 ml of whole blood to test for diseases. Our capture and handling procedures followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the South Dakota State University Institutional Animal Care and Use Committee (Approval No. 07-A024).

Home Areas

We used homing techniques from fixed winged aircraft (aerial telemetry, Samuel and Fuller 1996) to determine the daytime locations of mountain lions 1 time/week. We calculated home areas by using the lifetime dataset for each animal, because every area

utilized by a mountain lion contributes to survival. We used Fixed Kernel methods (Worton 1989) in ArcGIS 9 (ESRI, Redlands, CA) to delineate the home area of each individual. We defined the home area of each animal by the utilization distribution bandwidth that fully encompassed all known locations, within a single area (no disjunct areas). However, in some instances the 95% utilization distribution resulted in disjunct areas, which we allowed to persist. Thus, depending on the distribution of locations, the bandwidth that fully encompassed all known locations for most animals was the 85% utilization distribution.

Housing Analysis

We used a geographic information system (GIS; ArcGIS 9 or Arcview 3.2, ESRI, Redlands, California) to analyze home area and housing layers. We obtained point files for all residences within Custer, Pennington, Lawrence, and Meade counties, South Dakota, from planning and zoning offices in Pennington (Pennington, Lawrence, Meade County data) and Custer counties. We merged residential point files and clipped only those areas overlying the Black Hills, to produce a single residential point file for the Black Hills, excluding Fall River County and the land area within Wyoming. We calculated 200-m buffers around each point to account for clustering of residences into small exurban communities (e.g., towns of Rochford, Rockerville) that are common within the Black Hills. We dissolved the 200-m buffers around each point, which resulted in a single layer of demarcated areas ≤ 200 m from a residence. We subjectively chose 200 m as our buffer because if a mountain lion (resting, moving, hunting, predated) is >200 m from a residence it might be less likely to be detected by the human

occupants of the residence or their family dog. In fact, mean distance to total visual obstruction for 164 feeding sites of white-tailed deer in the Black Hills was 52.2 m, with sites associated with other behaviors and random sites having less distance (DePerno 1998). Mountain lions come into conflicts with humans or domestic pets, when they are perceived to be in proximity to personal property (e.g., buildings, livestock, domestic pets). Mountain lions that were detected by residents might be more likely to be reported to authorities (i.e., conflicts), which depending on location and circumstances the authorities might act to lethally remove the detected individual. Thus, mountain lions that have more of their home areas $>200\text{m}$ from a residence might have differing survival rates than animals with less area $>200\text{m}$ from a residence.

Home Areas and Housing Areas

We placed each animal's home area over the Black Hills housing area (areas ≤ 200 m from a residence) and calculated the proportion (recorded as percent [%]) of the animal's home area that was ≤ 200 m from a residence. For this analysis, we used only adult animals. Cubs were rarely found in conflict with residences and therefore, we did not expect housing to influence the survival of cubs. Interactions between subadults and residences occurs (Chapter 2); however, movements of subadults are erratic and determining the differences in interactions with humans is unlikely due to the lack of home areas and long-distance movements (Thompson 2009). In contrast, adult animals in our study area exhibited site fidelity, were occasionally in conflict, and occupied a range of residential densities and associated areas ≤ 200 m from a residence.

Disease Testing

We collected ocular samples by placing one synthetic swab under each of the 3 eyelids (upper, lower, and third) per eye producing 2 swabs per animal sampled. We collected whole blood by venipuncture of the medial saphenous or cephalic vein. Aliquots of ocular and blood samples were shipped to the Center for Companion Animal Studies in the Department of Clinical Sciences at Colorado State University by overnight express on ice. The samples were either processed on arrival or were frozen at - 80°C until assayed. Total DNA and RNA were extracted from whole blood and ocular swabs and evaluated for selected pathogens using previously reported assays. Molecular assays for amplification of DNA of feline herpesvirus 1 (FHV-1), DNA of *Mycoplasma* spp., DNA of *Chlamydophila felis*, and RNA of feline calicivirus (FCV) were performed on ocular samples (Low et al. 2007). Total DNA extracted from blood was evaluated in a PCR assay that amplified the DNA of haemotropic mycoplasmas (Jensen et al. 2001); an assay that amplified the DNA of *Ehrlichia* spp., *Anaplasma* spp., *Neorickettsia* spp., *Wolbachia* spp. (Lappin et al. 2004); and an assay that amplified the DNA of *Bartonella* spp. (Jensen et al. 2000). Samples positive for DNA of the *Ehrlichia/Anaplasma/Neorickettsia/Wolbachia* group, DNA of *M. haemofelis*, or DNA of *Bartonella* spp. were to be evaluated by genetic sequencing to further determine the infective species using a commercially available service (Macromolecular Resources, Colorado State University, Fort Collins, CO).

Serum antibodies against feline leukemia virus and feline immunodeficiency virus were measured by use of a commercially available kit marketed for use with samples

from domestic cats (SNAP® FeLV/FIV, Idexx Laboratories, Portland ME) following the manufacturer's instructions. Serum antibodies against *Toxoplasma gondii* and *Bartonella* spp. were measured by previously reported microELISA (Vollaire et al. 2005, Lappin et al. 2009). Serum neutralization assays were used to detect antibodies against FCV, FHV-1, and canine distemper virus. Antibodies against canine or feline parvoviruses were measured by hemagglutination inhibition; whether the antibodies were induced by exposure to dog or cat strains cannot be determined. The serum neutralization and hemagglutination inhibition assays were performed by the Veterinary Diagnostic Laboratory at Colorado State University. This laboratory is accredited (full service, all species) by the American Association of Veterinary Laboratory Diagnosticians (AAVLD) meeting standards based on ISO17025 / OIE (<http://dlab.colostate.edu/>) and is also a member of the National Animal Health Laboratory Network (NAHLN). Antibodies against *Yersinia pestis* were measured by an agglutination assay performed by the Centers for Disease Control in Fort Collins, Colorado.

Statistical Analysis

We used a known-fate model in Program MARK (White and Burnham 1999) to estimate survival rates. We used proportion of home area ≤ 200 m from a house (continuous) and sex (categorical) as covariates. We graphed survival curves by sex to investigate the role of housing on survival of mountain lions. We used logistic regression to investigate relationships between the proportion of home area ≤ 200 m from a house and exposure to specific diseases. For statistical analyses, we used JMP 8 (SAS Institute, Cary, NC).

RESULTS

We used data for 74 (19M, 53F) mountain lions that we had both survival data and information regarding housing throughout each animal's home area. Mean home area sizes for male and female mountain lions were 322.9 km² (95% C.I. = 179.2–466.6) and 99.4 km² (95% C.I. = 77.3–121.6), respectively. Mean housing densities within each animal's home area were 2.72 houses/km² and 2.78 houses/km² for males and females, respectively. Ranges for housing densities in our study area were 0–13.3 and 0–16.2 houses/km² for males and females, respectively. Housing densities did not differ between sexes ($F_{1,77, \alpha=0.05} = 0.005$, 1-sided $P = 0.945$). Mean proportion of area ≤ 200 m from a house within mountain lion home areas was 9.3% (95% C.I. = 5.4–13.2) and 9.7% (95% C.I. = 7.5–11.9) for males and females, respectively. Proportion of area ≤ 200 m from a house ranged from 0–27.3% and 0–33.6% of home areas of male and female mountain lions, respectively.

Annual mountain lion survival declined inversely as a function of the proportion of home area ≤ 200 m from a residence. Annual survival was described by the equation

$$\text{Logit}[S_{(i)}] = 4.8304 - 0.0597(\text{proportion of home area } < 200 \text{ m}) - 0.9696 (\text{sex}; M = 1, F = 0)$$

$$\text{where Survival} = e^{(\text{logit})} / 1 + e^{(\text{logit})}$$

Projected survival rates of adult male and female mountain lions declined to below 0.80 when the proportion of home area ≤ 200 m from a residence reached 40% and 60%, respectively (Figure 4.1).

We found 7 disease organisms in >10% of male or female blood samples, whereas another 5 disease organisms were rarely detected (Table 4.2). We found no relationships between proportion of home area $\leq 200\text{m}$ from a residence and presence of disease organisms in mountain lions (Table 4.2).

DISCUSSION

Our results regarding survival of mountain lions were similar to those from California. We found much variation in the amount of development that occurred in mountain lion home areas, ranging from none to 33% of home area $\leq 200\text{m}$ from a residence. Mountain lions in southern California showed individual variation in habitat use, as well, with some animals avoiding exurban development and some animals showing ambivalence (Burdett et al. 2010). Similarly, mountain lion survival was lower with increasing proportions of home areas $\leq 200\text{m}$ from a residence. Burdett et al. (2010) reported that mountain lions that were ambivalent to exurban development exhibited lower survival than those that avoided exurban areas. Adult mountain lions in remote areas largely void of human residences can exhibit annual survival rates > 0.80 (Logan and Sweanor 2001, Laundré and Hernández 2007). We found survival rates declined to < 0.80 for adult male and female mountain lions with $> 40\%$ and $> 60\%$ of the home area $\leq 200\text{m}$ from a human residence. These results suggest that relatively low density housing, typical of exurban landscape developments negatively affect mountain lion behavior and survival (Burdett et al. 2010).

We showed that disease exposures in adult mountain lions exhibited no relationship to amount of home area $\leq 200\text{ m}$ from a residence. Housing densities in the

Black Hills might be too high to detect a relationship to disease exposures in adult mountain lions. We found few animals occupying areas with no human residences, whereas in areas of the western United States more mountain lions could be sampled with home areas void of human residences. Landscape-level movement patterns (e.g., immigration/emigration) exhibited by mountain lions and the persistence of titers for diseases within immune systems result in mountain lions exposed to diseases within natal areas or during transient movements to adult home areas that might show no resemblance in housing densities.

Clearly, exposure rates were high for several diseases (e.g., parvo virus); however, little is known about mountain lion disease prevalence in large areas away from human residences. Parvo virus exposure is consistently high among mountain lions from California, Rocky Mountains, and Florida and is thought to be endemic within mountain lion populations (Roelke et al. 1993, Paul-Murphy et al. 1994, Biek et al. 2006). This pattern suggests that human residential density does not likely play a role in exposure rates among mountain lions, but might play a role in exposure pathways from wildlife to domestic cats and dogs. Low rates of exposure to other diseases occurred in Black Hills mountain lions, which was similar to other studies (Roelke et al. 1993, Paul-Murphy et al. 1994, Beik et al 2006). Those diseases are generally environmentally fragile and require direct contact between animals for transmission. Other researchers suggested the solitary nature of mountain lions and disease fragility and transmission explained low prevalences.

LITERATURE CITED

- Anderson, C. R., Jr., and F. G. Lindzey. 2000. A guide to estimating mountain lion age classes. Wyoming Cooperative Fish and Wildlife Research Unit: Laramie, Wyoming, USA.
- Baron, J., S., D. M. Theobald, and D. B. Fagre. 2000. Management of land use conflicts in the United States Rocky Mountains. *Mountain Research and Development* 20:24–27.
- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:446–471.
- Burdett, C. L., K. R. Crooks, D. M. Theobald, K. R. Wilson, E. E. Boydston, L. M. Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. *Ecosphere* 1:1–21.
- DePerno, C. S. 1998. Habitat selection of a declining white-tailed deer herd in the central Black Hills, South Dakota and Wyoming. Dissertation, South Dakota State University, Brookings, SD.
- Froiland, S. G. 1990. Natural history of the Black Hills and Badlands. The Center for Western Studies, Sioux Falls, South Dakota, USA.
- Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.

- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* 21: 1–39.
- Kertson, B. N., R. D. Spencer, and C. E. Grue. 2008. Demographic and landscape influences on the cougar-human interaction in western Washington. *Proceedings of the Ninth Mountain Lion Workshop* 9:111.
- Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. International Wildlife Veterinary Services. Laramie, Wyoming, USA.
- Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains: a field guide with color photographs. Fenske Media Corporation, Rapid City, SD, USA.
- Laundré, J. W., L. Hernández, and S. G. Clark. 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. *Journal of Wildlife Management* 71:345–355.
- Logan, K. A., and L. L. Swenar. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC.
- Logan, K. A., L. L. Swenar, J. F. Smith, and M. G. Hornocker. 1999. Capturing pumas with foot-hold snares. *Wildlife Society Bulletin* 27:201–208.
- Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2003. Biodiversity across a rural land-use gradient. *Conservation Biology* 17:1425–1434.
- Nicholson, K. L. 2009. Spatial movements and ecology of mountain lions in southern Arizona. Dissertation, University of Arizona, Tucson, AZ, USA.

- Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conservation Biology* 15: 1143–1150.
- Orlando, A. M. 2008. Impacts of rural development on puma ecology in California's Sierra Nevada. Dissertation. University of California, Davis, USA.
- Theobald, D. M. 2003. Targeting conservation action through assessment of protection and exurban threats. *Conservation Biology* 17:1624–1637.
- Thompson, D. J. 2009. Population demographics of cougars in the Black Hills: survival, dispersal, morphometry, genetic structure, and associated interactions with density-dependence. Dissertation. South Dakota State University, Brookings, South Dakota, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–139.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70: 164–168.

Table 4.1. Cities within and along the perimeter of the Black Hills, 2006–2009.

City, State	Approximate Population (US Census Bureau 2000)	Location	Latitude	Longitude
Hulett, WY	400	Interior	44.68613°	104.60048°
Spearfish, SD	8,600	Perimeter	44.48868°	103.84757°
Sundance, WY	1,100	Perimeter	44.40459°	104.37480°
Whitewood, SD	800	Perimeter	44.46155°	103.64054°
Sturgis, SD	6,400	Perimeter	44.41160°	103.51523°
Deadwood, SD	1,300	Interior	44.38196°	103.72399°
Lead, SD	3,000	Interior	44.35213°	103.76748°
Piedmont, SD	250	Perimeter	44.23338°	103.39177°
Rapid City, SD	60,000	Perimeter	44.07509°	103.23346°
Hill City, SD	780	Interior	43.93208°	103.57209°
Keystone, SD	300	Interior	43.89327°	103.42466°
Newcastle, WY	3,000	Perimeter	43.85483°	104.20445°
Custer, SD	1,800	Interior	43.76643°	103.60140°
Pringle, SD	125	Interior	43.60905°	103.59437°
Hot Springs, SD	4,100	Interior	43.43262°	103.48098°

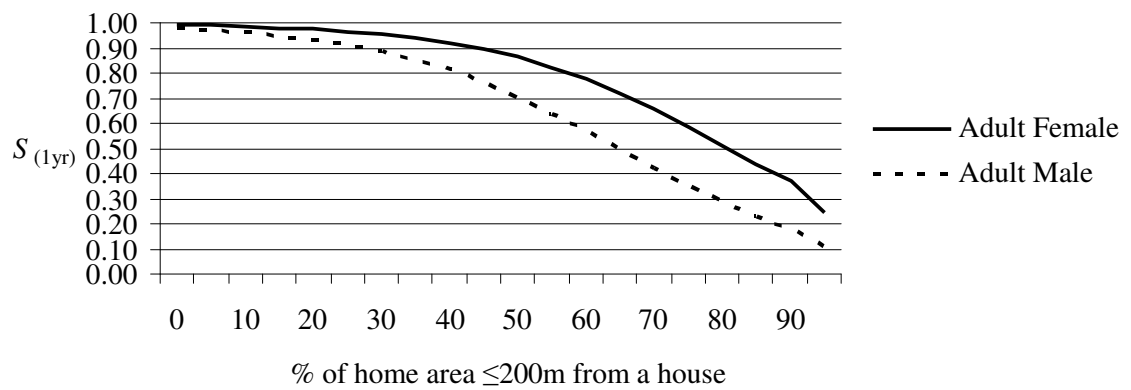
Table 4.2. Prevalence of 12 disease organisms in mountain lions from the Black Hills, South Dakota, 2006–2009. Logistic Regression of disease exposure and the proportion of home area ≤ 200 m from a residence for mountain lions in the Black Hills, South Dakota. Disease organisms that were tested were Feline Immunodeficiency Virus (FIV), Feline Calici Virus (FCV), Feline/Canine Parvo Virus (F/CPV), Canine Distemper Virus (CDV), *Toxoplasma gondii* (*T. gondii* IgG-specific test), *Mycoplasma haemominutum* (*M. haemominutum*), *Bartonella* spp. IgG-specific test, Feline Leukemia Virus (FLV), Feline Herpes Virus (FHV), Plague, *Ehrlichia* spp., and *Mycoplasma haemofelis* (*M. haemofelis*),

Disease Organism	Sex	No. Positive/Tested	Proportion Positive (%)	95% Confidence Interval (%)	Logistic Regression X^2, P
FIV	M	4/39	10.3	4.1 – 23.6	1.12, 0.289
	F	8/57	14.0	7.3 – 25.3	
FCV	M	8/36	22.2	11.7 – 38.1	2.00, 0.158
	F	15/49	30.6	19.5 – 44.5	
F/CPV	M	27/36	75.0	58.9 – 86.2	3.89, 0.049
	F	42/49	85.7	73.3 – 92.9	
CDV	M	6/36	16.7	7.9 – 31.9	0.06, 0.801
	F	8/49	16.3	8.5 – 29.0	

Table 4.2. continued

Disease	Sex	No.	Proportion	95% Confidence	Logistic
Organism		Positive/Tested	Positive (%)	Interval (%)	Regression
					χ^2, P
<i>T. gondii</i> IgG	M	18/39	46.2	31.6 – 61.4	1.22, 0.270
	F	33/58	56.9	44.1 – 68.8	
<i>M. haemominutum</i>	M	21/39	53.8	38.6 – 68.4	0.44, 0.507
	F	43/58	74.1	61.6 – 83.7	
<i>Bartonella</i> spp. IgG	M	4/39	10.3	4.1 – 23.6	0.18, 0.672
	F	3/58	5.2	1.8 – 14.1	
FLV	M	1/39	2.6	0.5 – 13.2	
	F	0/57	0		
FHV	M	1/36	2.8	0.5 – 14.2	
	F	0/49	0		
Plague	M	0/32	0		
	F	0/36	0		
<i>Ehrlichia</i> spp.	M	2/39	5.1	1.4 – 16.9	
	F	1/58	1.7	0.3 – 9.1	
<i>M. haemofelis</i>	M	0/39	0		
	F	1/58	1.7	0.3 – 9.1	

Figure 4.1. Survival curve of adult mountain lions (*Puma concolor*) in relation to the proportion of home areas ≤ 200 m of a residence in the Black Hills, South Dakota, 2003–2009.



CHAPTER 5. SOME OBSERVATIONS OF MOUNTAIN LIONS

INTRODUCTION

During the course of any significant field-based research project, observations occur that generate thought, interest, and sometimes further inquiry. My research experience was no less similar and I have spent many hours wondering about what I saw and investigated. This chapter was written at the request of my research committee. Most of these are not statistically defensible, I recognize that, but for the most part they might invoke thought and consideration by future work and perhaps they might be the beginnings of more detailed investigation.

HOME AREA SIZES OF ADULT MOUNTAIN LIONS IN THE BLACK HILLS

METHODS

Home Area Size

I used only adult animals that were followed for ≥ 12 months to calculate annual home area sizes. I (and others) located animals at least bi-weekly by aerial telemetry and recorded the location with a GPS. I calculated home area sizes by using the Animal Movement extension in Arcview 3.2. I used Fixed Kernel methods and declared the home area as being the 95% Utilization Distribution. I determined the region of the Black Hills occupied by an animal if $>50\%$ of its home area was in 1 of 4 quadrants of the South Dakota Black Hills. In 1 case, an adult female's home area was entirely in the Wyoming Black Hills, and so she was excluded from analysis of home area sizes. For adult animals that were followed for >1 year, I calculated multiple home areas by year. I then calculated a mean annual home area for each animal with >1 year of data.

Statistics

I divided adult animals by sex and used Analysis of Variance (ANOVA) to determine if home area sizes varied regionally within the South Dakota Black Hills. Where the results of ANOVA suggested there was a difference in home area sizes by region, I used an Extra Sums-of-Squares *F*-test to determine which region (Northwest [NW], Northeast [NE], Southwest [SW], Southeast [SE]) animals maintained the largest home areas. I used multiple regression to investigate the change in home area sizes for adults over time, while accounting for any variation by region. I used region of the Black Hills occupied and year as covariates for adult males and females. I used the natural log transformation of annual home area size to analyze home area sizes, however I report results in standard measurements.

RESULTS

I calculated annual home area sizes for 16 adult males for which we had >12 months of location data, from 2002–2009; of which, 8 adult males were followed for ≥ 1 year. I calculated annual home area sizes for 42 adult females for which we had >12 months of location data, from 2002–2009; of which 26 adult females were followed for ≥ 1 year.

I found that adult male home area sizes were not similar across the study area. After accounting for variation by year, I found evidence that home area sizes for adult males varied regionally ($F_{(1,3)} = 5.43$, 2-sided $P = 0.013$). I found home area sizes were $314.2 \text{ km}^2 \pm 1.4$ (SE), 533.8 ± 1.4 , 804.3 ± 1.5 , 317.3 ± 1.4 for adult males residing in the NW, NE, SW, SE, respectively. Adult males that lived in the southwestern quarter of the

Black Hills maintained larger annual home areas than conspecifics in other areas (Extra sums-of-squares $F_{(1,20)} = 13.64$, 2-sided $P = 0.003$, Figure 5.1).

After accounting for yearly variation, I found strong evidence that adult female home area size varied regionally ($F_{(1,3)} = 9.913$, 2-sided $P < 0.001$, Figure 5.2). I found home area sizes were $80.6 \text{ km}^2 \pm 1.6$ (SE), 66.0 ± 1.5 , 198.3 ± 1.6 , 102.5 ± 1.5 for adult females residing in the NW, NE, SW, SE, respectively. Adult females that lived in the southwestern quarter of the Black Hills maintained larger annual home areas than conspecifics in other areas (Extra sums-of-squares $F_{(1,82)} = 20.23$, 2-sided $P < 0.001$).

CAUSES OF CUB MORTALITY

The dominant cause of mortality for mountain lion cubs is from direct killing by other mountain lions (Logan and Sweanor 2001, Cooley et al. 2009). These studies used indirect methods to assign cause of death such as the presence of tracks, scat, evidence of burial, and scrapes. Indirect evidence is necessary because mountain lions are secretive, nocturnal, and nearly impossible to observe. I radiocollared 103 (47♀, 56♂) mountain lion cubs within natal dens to assess survival with expandable radiocollars similar to ones used in previous studies. During this research, I investigated 27 deaths. Because I was using very high frequency (VHF) radio transmitters and aerial telemetry one time per week, I was unable to know time of death, prior to investigations. There were 2 investigations that revealed information about evidence of mortality.

On 13 September 2007, aerial relocation of F159 revealed a radio signal suggesting a mortality or collar failure. That afternoon, I investigated the site and found the mother (F85) present at the site and assumed the collar had dropped off of F159. I

returned the following day to collect the collar and found no radio signal from F85. I located the questionable collar under a spruce tree along with the remains of F159's face, abdomen, and feet. I concluded that a predator, likely another mountain lion, had killed F159.

On 19 October 2007, aerial relocation of M156 revealed a radio signal suggesting a mortality or collar failure. That afternoon, I investigated the scene and by using radio telemetry determined that the mother (F130) and sister (F157) were still at the site of the questionable collar. Because of their presence, I assumed that the collar had failed and that it had dropped off of M156 and that no mortality had occurred. I returned to the vicinity the following day to retrieve the collar. However, I again found the radio signals of F130 and F157 at the site and so I decided to return the next day. On 21 October 2007, I returned to the site, where the radio signal was originating and found the dead body of M156 and it was clearly multiple days old. Because of the snow on the ground, I found numerous tracks of the mother and sister, as expected, but also did not find any evidence of external trauma. Internal organs were intact with 1 lung being filled with coagulated blood; normal appearance of lung tissue is pink, but often the downward lung is filled with blood after mortality and so it is normally darker in color. This mortality was considered an accident of unknown cause, but that capture 6 weeks prior was unrelated. I also considered the mortality as not having been caused by a predator.

Most mountain lion research has been conducted in environments where tracks are difficult to observe (e.g., coniferous forests), except during periods with snow cover on the ground. Standard procedure has been to use the presence of sign to indicate cause

of death and when predation is concluded, which predator species killed the animal. In 2 cases, I found the mother of the cub to have been present for some period of time at the scene indicating either the mother killed the cub in 1 event or the mother remained with the cub long after death. If mothers routinely remain at the site of death, then presence of sign can not be used to reliably indicate infanticide. Because mountain lion cubs are small, they are presumably vulnerable to many other predator species, and the declaration of infanticide is tenuous.

EMIGRATION BY AN ADULT FEMALE

On 9 February 2007, personnel from South Dakota Department of Game, Fish, and Parks and I captured a 44.1 kg (97 lbs) female (F112) that had not lactated previously and was determined to be approximately 2 yrs of age. On 5 July 2007, I captured 3 male cubs in F112's natal den and placed radiocollars on each of them. I determined based on aerial telemetry of F112 and tooth eruption that the cubs were approximately 3 weeks of age and they weighed 1.5–2.2 kg. On 7 August 2007 (4 weeks later), radio telemetry signals suggested a mortality event of 1 cub. When I located the remains of M141, I found parts of his body, the radiocollar, tracks and scat nearby. I assumed the mortality was by another mountain lion, although low populations of coyote (*Canis latrans*), bobcat (*Lynx rufus*), domestic dog, and domestic cat do occur in the Black Hills. At the time of the investigation, the mother F112 was about 200 m away, with her 2 remaining cubs. Eight days later, on 15 October 2007, I detected 2 more mortality events to F112's cubs and immediately investigated. At this scene, I found both collars and the body parts of 1 cub. However, I found no evidence of the 3rd cub and assumed he might have

escaped. Again, the evidence suggested that another mountain lion killed this cub. After 15 August 2007, I relocated F112 2 more times until 30 August 2007, the last location of F112. Because radiocollar occasionally failed to transmit and F112 was an adult and might have 1 cub, I assumed that her collar prematurely failed. On 31 December 2007, F112 was killed by a hunter approximately 64 km west of Broadus, Montana. That location was approximately 250 km from her last known location and across 100 km of prairie grasslands in the Powder River Basin.

Only 1 other case of an adult female mountain lion dispersing has been described (Maehr et al. 1989). In Florida, an adult female produced a litter of cubs and then dispersed 16 km away. This case in Florida was similar to F112 in that dispersal occurred following the loss of the first litter. However, F112 emigrated out of the ecological population, after having traversed at least 140 km of habitat.

ORPHAN CUBS

I radiocollared 103 (47♀, 56♂) mountain lion cubs that varied in ages from 2–6 weeks of age with expandable radiocollars. Of those 103 cubs, 12 of them were orphaned as a result of sport-hunting. Cubs were orphaned at various ages from 10 (~2.5 months)–34 weeks (~8.5 months). The 3 youngest cubs from a single litter (10 weeks of age) were retrieved by South Dakota Department of Game, Fish, and Parks personnel and sent to various zoological parks. There were 3 that disappeared due to collar failure. Of the 6 remaining cubs, 1 was orphaned at 4.25 months of age and she survived to the age of 17 months, when she was also killed by a sport-hunter the following season. There were 3 cases of orphaned cubs that were killed by humans. One cub was orphaned at 4–5

months of age and he was killed at 11 months of age after he was discovered in town. One cub was orphaned at 4.75 months of age and later killed by a homeowner in a justified shooting incident at 6 months of age. The final cub was orphaned at 8.5 months of age and her collar was located within 3 days of orphaning in the vicinity of the mothers mortality site. The collar was alongside a paved roadway with the material cleanly cut and blood on the collar and I strongly suspect that she was killed. There were 2 cases of cubs being killed by other mountain lions. One cub was orphaned at 4.75 months of age and his radiocollar was found inside a large mountain lion scat. He would have been 9 months of age at the time of death. Another cub was 6.75 months of age when he was orphaned and he was found dead at 8 months of age. There was only pieces of his skull and feet remaining and there were large mountain lion tracks in the snow at the mortality site.

SATELLITE CUBS

I observed 2 instances where I observed cubs of different ages and adult females feeding at a kill-site at the same time. In one case, I had radiocollared and tattooed an entire litter of 3 cubs (1♂, 2♀) and 4 weeks of age. Because of the circumstances of the capture, all cubs were captured and there was no opportunity of escape by any. I later found 1♀ dead at 3.25 months of age. The remaining 2 survived and at 7 months of age, I located the family of 3 (2 cubs, 1 mother) feeding on a roadkilled deer that I had placed to capture mountain lions. I placed a motion-sensitive infrared camera at the site and recorded 3 cubs and 1 adult female feeding on the carcass at the same time. One of the cubs was obviously smaller than the other 2, even though there were 1 of each sex

known. When the radiocollared cubs were 11.5 months of age, I again detected the family on a roadkilled deer and this time I recaptured them to replace their collars. During that recapture, I captured the mother, her 2 cubs (age = 11.5 months), and I also captured another female cub that was aged at 10 months. This cub did not have eartags or tattoos, as did the cubs born to the adult female. The relationship of the cub to the family is unknown, however she was not the littermate of the 2 other cubs.

Another cases involved an unknown family group. Cory Mosby, a fellow graduate student, detected a freshly killed deer and observed mountain lion tracks in the snow. I placed a motion-sensitive camera on the site and detected 2 apparently emaciated cubs and 1 much larger cub along with an adult female. I captured all of the individuals during a single capture attempt. I found an adult female, a male cub that was 10 months of age, and 2 (1♂, 1♀) cubs that still had deciduous canine teeth and were thought to be <8 months of age. The older male cub weighed 31.8 kg (70 lbs), whereas the emaciated male and female weighed 20 kg (40 lbs) and 14.1 kg (31 lbs). A week later, the mother and male cub were far from the capture site, whereas the 2 emaciated cubs were still in the vicinity of the capture site and 1 female was found dead within 200 m of the site 2 months following capture.

These cases are different in that 1 family apparently permitted a satellite cub to follow the family, whereas 1 other case involved satellite cubs feeding at a site, but not following the family. In both cases, there was evidence of an adult female allowing an unrelated mountain lion to feed at a site along with her offspring.

LITERATURE CITED

- Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology* 90:2913–2921.
- Logan, K. A., and L. L. Swenar. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC.
- Maehr, D., J. C. Roof, E. D. Land, and J. W. McCowan. 1989. First reproduction of a panther (*Felis concolor coryi*) in southwestern Florida, U.S.A. *Mammalia* 53:129–131.

Figure 5.1. Regional variation in home area sizes of adult male (>3 yrs of age) mountain lions (*Puma concolor*) in the Black Hills, South Dakota from 2003–2009.

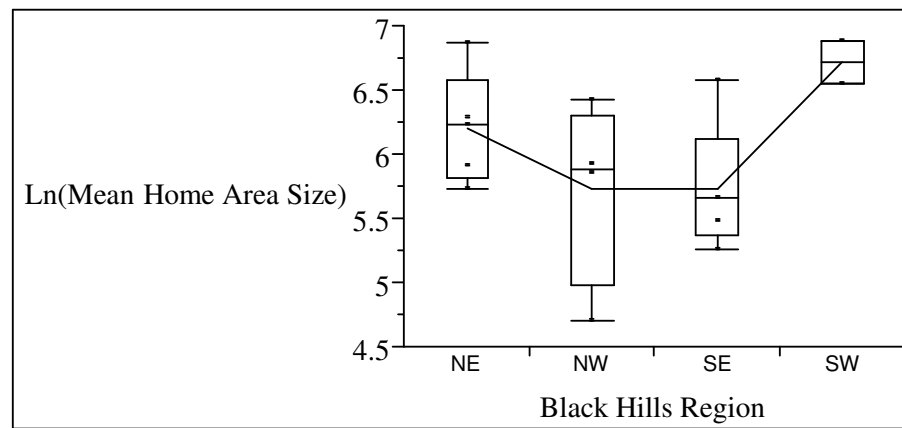


Figure 5.2. Regional variation in home area sizes of adult female (>3 yrs of age) mountain lions (*Puma concolor*) in the Black Hills, South Dakota from 2003–2009.

