

**EFFECTS OF HUNTING ON COUGAR POPULATION DEMOGRAPHY**

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the dissertation of  
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# EFFECTS OF HUNTING ON COUGAR POPULATION DEMOGRAPHY

## Abstract

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Hunting is commonly used by wildlife agencies to provide recreational opportunities and to reduce human/wildlife conflicts. Game managers rely on accurate population estimates to assess population trends and effectiveness of management decisions.

Because such direct counts are difficult to achieve for cougar populations, managers often use survival and fecundity models to assess effects of hunting. Many of these rate-based models assume a closed population structure, whereby emigration and immigration are balanced or considered unimportant. However, for large carnivores, which have large home ranges and disperse long distances, an open population structure may be more appropriate. From 2001 – 2008, I investigated the effects of hunting on two Washington cougar populations (one heavily hunted and one lightly hunted) using both survival/fecundity models and density estimates derived from direct counts. In the lightly hunted population, survival/fecundity rates predicted a 10% annual population increase, whereas direct counts indicated a stable population. In the heavily hunted population, the survival/fecundity model predicted a 27% decrease, but counts revealed only a 9% annual decrease. We believe the difference between the predicted and observed growth rates was likely caused by immigration and emigration. High hunter harvest triggered immigration, decreased female numbers, and produced a younger overall age structure. Low hunter harvest triggered emigration, stable female numbers,

and resulted in an older overall age structure. These results suggest that cougar populations may be self-regulating, and that traditional survival/fecundity harvest models are unable to accurately predict the population responses to hunting.

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## Dedication

To my family.

Skye, for patiently providing, and for your intellectual guidance and loving companionship. Mum and dad, for your sacrifices, unconditional love, and support. Courtney and Tyler, for your advice, encouragement, and love. Emma, for the joy that you've brought into my life.

**CHAPTER ONE**

**SOURCE POPULATIONS IN CARNIVORE MANAGEMENT: COUGAR**

**DEMOGRAPHY AND EMIGRATION IN A LIGHTLY HUNTED POPULATION**

## **ABSTRACT**

Wildlife agencies typically attempt to manage carnivore numbers in localized game management units through hunting and do not always consider the potential influences of immigration and emigration on the outcome of those hunting practices. However, a closed population structure may not be an appropriate model for management of carnivore populations where immigration and emigration are important population parameters. A closed population hypothesis predicts that high hunting mortality will reduce numbers and densities of carnivores and that low hunting mortality will increase numbers and densities. By contrast, the open population hypothesis predicts that high hunting mortality may not reduce carnivore densities because of compensatory immigration, and low rates of hunting mortality may not result in more carnivores because of compensatory emigration. Previous research supported the open population hypothesis in a heavily hunted (hunting mortality rate = 0.24) cougar population in northern Washington. I test the open and closed population hypotheses in a lightly hunted (hunting mortality rate = 0.11) cougar population in central Washington by monitoring demography from 2001 to 2007. I used a dual sex survival/fecundity Leslie matrix to estimate closed population growth and annual census counts to estimate open population growth. The observed open population growth rate of 0.98 was lower than the survival/fecundity growth rates of 1.13 (deterministic) and 1.10 (stochastic), and may result from a 12-15% annual emigration rate. My data supports the open population hypothesis for lightly hunted populations of carnivores. Low hunting mortality did not result in increased numbers and densities of cougars.

## INTRODUCTION

Sport hunting is commonly used to manage populations of large herbivores, such as white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*, Bolen and Robinson 2003, Sinclair et al. 2006). Large carnivores such as cougars (*Puma concolor*), black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), and leopards (*Panthera pardus*) are similarly hunted for sport and population control (Treves and Karanth 2003). Managers commonly believe that sport hunting is effective for reducing the size of carnivore populations, the amount of predation on game species, and the number of human/carnivore conflicts (Treves and Karanth 2003, Strickland et al. 1994).

Wildlife agencies typically attempt to manage carnivore numbers in localized game management units through hunting and may not consider the potential influences of immigration and emigration on the outcome of those hunting practices (Cougar Management Guidelines Working Group 2005:42-44). This closed population paradigm predicts that hunting will reduce animal numbers and densities, and human/carnivore conflicts within a game management unit (Strickland et al. 1994). The corollary is that light hunting pressure, will increase numbers and densities of carnivores and human/carnivore conflicts. However, long-distance dispersal is an important aspect of carnivore population ecology (Chepko-Sade and Halpin 1987, Howe et al. 1991, Franke and Woodroffe 2001, Zimmerman et al. 2005, Whitman et al. 2007). High rates of emigration can depress population growth, and high rates of immigration can increase population growth regardless of birth and death rates. Failure to consider these dynamics may preclude achievement of management objectives for carnivores.

Cougars are hunted for sport and population control throughout the western U.S. based on the closed population hypothesis (Cougar Management Guidelines Working Group 2005:71-82, Strickland et al. 1994). However, young male cougars exhibit intrinsic, long-distance dispersal (Logan and Sweanor 2001, Sweanor et al. 2000, Ross and Jalkotzy 1992), suggesting that the open population hypothesis may be more appropriate. A previous study showed that high hunting mortality of cougars (hunting mortality rate = 0.24) within a small scale (< 1000 km<sup>2</sup>) management unit did not result in the expected population decline because of compensatory immigration. Those results supported the open population hypothesis in a heavily hunted cougar population in northeast Washington (Robinson et al. 2008).

I test the open and closed population hypotheses for a lightly hunted (hunting mortality rate = 0.11) cougar population from 2001 to 2007 in central Washington. I compare a closed population growth model based on survival/fecundity rates to open, observed rates of population growth over a 6 year period. I test whether low hunting mortality results in high population growth, as commonly believed (closed population hypothesis) or if low mortality is counterbalanced by compensatory emigration (open population hypothesis), as predicted by Robinson et al. (2008).

## **STUDY AREA**

The 594-km<sup>2</sup> study area, located on the east slope of the North Cascades near the town of Cle Elum, Washington, included a patchwork of public (U.S. Forest Service, Washington Department of Fish and Wildlife, Washington Department of Natural Resources) and private lands, with rural residential development and agriculture

dominating the valley bottoms (Fig. 1). The study area included the upper Yakima River watershed with the Cascade Range bordering the study area on the west, the Enchantment Wilderness to the north, and agricultural lands in the Kittitas Valley to the southeast. Part of the Cascade Mixed Forest ecoregion (Bailey et al. 1994), the area rises from sagebrush steppe, ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) in the foothills (550 m), to sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) at higher elevations (1550 m). Average winter temperature from December to February is 1.2°C and average summer temperature from June to August is 17.6°C. Precipitation averages 56.4 cm/yr, with the majority falling in winter as snow (average winter snowfall is 160cm).

Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species besides cougars include coyotes (*Canis latrans*), black bears, and bobcats (*Lynx rufus*). Cougar harvest without the use of hounds was permitted in the study area each year of the study from 1 August to 15 March.

## **METHODS**

To allow comparisons with the heavily hunted population (Robinson et al. 2008) I used the same methods for all aspects of this study.

## Captures and Monitoring

I attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of the entire study area during winter when tracks are detected in snow. I used hounds to track and tree cougars in winter (Hornocker 1970). I immobilized treed cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL), at a dosage of 0.4 mL/10 kg of body mass, using a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). I determined sex by examining visible genitalia and age from measurements of gum regression (Laundre et al. 2000). I assigned age classes as kitten (0-12 months), juvenile (13-24 months), and adult (25+ months).

I fitted each animal with a mortality-sensing Very High Frequency (VHF, Advanced Telemetry Systems, Isanti MN) or Global Positioning System (GPS, Lotek Wireless Inc, Newmarket, Ontario and Televilt, Lindesberg, Sweden) collar. Beginning in January 2005, I investigated den sites of GPS-collared females, and captured kittens by hand. I collared kittens that were > 6-weeks old with expandable VHF (Telonics Inc, Mesa, AZ; T. Ruth personal communication 2004) radio collars. I handled all animals in accordance with Washington State University Animal Care (IACUC permit 3133) and Animal Welfare Assurance Committee (permit A3485-01). I recorded locations of VHF-collared animals at one week intervals from ground or aerial telemetry, and of GPS-collared animals from remote retrieval of 4 hour interval satellite location data.

Despite attempts to systematically search and mark animals, I was not able to mark the entire population. Therefore, to establish a minimum population estimate for each area I included demographic data from collared and uncollared cougars that were

harvested in the area, and those killed during reported encounters with humans, conflicts with livestock, or from collisions with vehicles (Stoner et al. 2006, Robinson et al. 2008). Washington Department of Fish and Wildlife recorded sex and age (determined by cementum annuli) for uncollared cougars killed by hunters or other causes. Because measurements of gum regression and cementum annuli yield comparable ages (Robinson et al. 2008), I included all collared and uncollared animals in a linear regression analysis to examine trends in age structure over the study period.

### Survival

I used radio-telemetry to monitor survival of all radio-collared cougars and assigned cause of mortality as hunting, vehicle, or natural. Natural mortalities were confirmed with necropsies. I inferred cause of kitten mortalities by examining the carcass and proximity to collared cougars.

I used the modified Mayfield method (Mayfield 1961, Heisey and Fuller 1985) to estimate survival of animals because it performs well for small sample sizes, and estimates seasonal and cause-specific mortality rates (Winterstein et al. 2001, Lambert et al. 2006, Murray 2007, Robinson et al. 2008). I estimated mean annual survival rates for male and female kittens, juveniles, and adults from 2002 to December 2007. To estimate annual environmental variation, I calculated a weighted average of demographic variance from pooled sex and age classes and then subtracted it from the total observed variance (Akçakaya's 2002). This estimate minimizes sampling error and accounts for demographic stochasticity.

I analyzed the statistical distribution of the deaths over a year (365 d) to determine the time intervals when survival probabilities were constant. This yielded 2 seasons: the high (1 Aug to 31 Dec) and the low mortality season (1 Jan to 31 July). Intervals for each period were chosen based on the median date of the deaths for each period. I used the Taylor series approximation method to compute variances of class-specific survival rates and tested for differences between classes with a two-tailed z-test (Micromort version 1.3, Heisey and Fuller 1985).

### Maternity and fecundity

I calculated maternity as the mean number of kittens divided by the number of adult females observed that year (Case 2000). I calculated fecundity rate,  $F = S_F \times M_{x+1}$  from the female survival rate in year x multiplied by their mean maternity rate the following year (Ebert 1999). To estimate annual environmental variation of fecundity rates, I calculated a weighted average of demographic variance and then subtracted it from the total observed variance (Akcakaya 2002). This estimate minimizes sampling error and accounts for demographic stochasticity.

### Deterministic and stochastic growth rates

I constructed a closed model of population growth from sex- and age-specific survival and fecundity rates and modeled population growth with a dual-sex Leslie matrix (Leslie 1945) in RAMAS GIS (Akcakaya 2002). Additional demographic parameters were: female age at first reproduction = 24 months; sex ratio at birth = 1:1; and maximum age and for age at senescence = 13 years (Logan and Sweanor 2001).

I calculated the deterministic growth rate ( $\lambda_D$ ) as the dominant eigenvalue of the matrix under a stable age distribution. I calculated the stochastic growth rate ( $\lambda_S$ ) by incorporating annual environmental variability (standard deviation of annual survival and fecundity rates) and demographic stochasticity. To estimate demographic stochasticity, I sampled the number of survivors in each sex and age class from a binomial distribution, and the number of kittens born each year from a Poisson distribution using the random number generator of RAMAS GIS (Akçakaya 2002). I sampled vital rates from a lognormal distribution to avoid truncations, which can occur if standard deviations are large due to sampling and measurement error. I projected the population for six years (five transitions), and calculated  $\lambda_S$  as the average geometric mean growth rate from 200 simulations, the point at which rates converged (Robinson et al. 2008).

#### Observed growth rate

I determined the observed growth rate ( $\lambda_O$ ) from annual counts of collared and unmarked cougars. Each year I tallied the number of cougars (adults, juveniles, and kittens) in the study area, and calculated the observed population growth rate,  $\lambda_O$ , as  $\lambda_x = (n_t / n_o)^{1/t}$  where  $\lambda_x$  is the annual finite growth rate,  $n_o$  is the starting population,  $n_t$  is the final population, and  $t$  is the number of transitions between the start and end of the population projection (Case 2000). I used a one-tailed, one-sample t test to determine whether deterministic ( $\lambda_D$ ) and stochastic ( $\lambda_S$ ) growth rates were higher than the average six-year observed ( $\lambda_O$ ) growth rate (Zar 1999). I estimated emigration rate ( $e$ ) using the equations  $e = \lambda_D - \lambda_O$  and  $e = \lambda_S - \lambda_O$  (Peery et al. 2006). I also used observations of

radio-collared cougars to document emigration and immigration from 2005 through 2007, the period during which I had accurate kitten survival data.

### Population density

I estimated mean annual density (cougars/100 km<sup>2</sup>) for collared and unmarked cougars present in the core study area (area annually searched for cougar tracks) from August 2001 through July 2007. Because the core area (594 km<sup>2</sup>) was small (and open) compared to the mean male home range size (416 km<sup>2</sup>), the estimate represented a maximum density, particularly for male density estimates. This provided a consistent measure of density among years and permits comparison to Robinson et al. (2008) who used the same methodology, but should not be compared to areas elsewhere. I back-calculated the lifespan of each marked and unmarked cougar to the beginning of the study, its birth date, or immigration date as described by Logan and Sweanor (2001:66), Stoner et al. (2006), and Robinson et al. (2008). I used linear regression to test for significant changes in density over the study period (Zar 1999).

## **RESULTS**

### Captures and Monitoring

I counted 74 cougars in the study area between January 2002 and December 2007. I collared 46 animals: 6 female and 13 male kittens, 1 female and 4 male juveniles, and 8 female and 14 male adults. I counted 28 unmarked cougars that were shot: 3 female and 1 male kitten, 2 female and 3 male juveniles, and 10 female and 9 male adults. One uncollared female died from a vehicle collision.

### Survival and Mortality

Eighteen of 46 radio-collared cougars were killed during the study period. Seven were killed by hunters, 3 died in collisions with vehicles, and 6 died of natural causes (Table 1.1). Six juvenile cougars (2 females, 4 males) emigrated out of the study area and I censored these on their last known date in the area. I censored an additional 7 animals after they shed their collars or lost VHF signals. I also censored 1 kitten that died 2 weeks after sustaining an injury during capture. Of 19 radio-collared kittens, 9 survived to dispersal age of 18 months (5 males, 4 females).

Average annual survival rate for all radio-collared cougars was  $0.71 \pm 0.06$ , but age and sex classes showed high variation (Table 1.2). Female survival ( $0.83 \pm 0.07$ ) was higher than male survival ( $0.60 \pm 0.09$ ,  $Z = 2.16$ ,  $p = 0.03$ ), and adult female survival ( $0.87 \pm 0.07$ ) was higher than adult male survival ( $0.65 \pm 0.11$ ,  $Z = 1.71$ ,  $p = 0.09$ ). I did not detect differences among other sex and age classes. I estimated environmental standard deviation of survival for all collared cougars at 0.05. Mortality from hunting was  $0.11 \pm 0.04$  and mortality from all combined causes was  $0.19 \pm 0.05$ .

### Maternity and fecundity

I estimated mean litter size at  $2.47 \pm 0.83$  from 15 litters. Proportion of females producing newborns was 0.45 and proportion of females with dependent kittens was 0.72. Mean maternity rate  $M_x$  was 1.12 kittens/ female/year. The fecundity rate  $F_x$  was  $0.49 \pm 0.22$  kittens of each sex per year. I estimated environmental standard deviation of fecundity at 0.27 female kittens per year.

### Population Growth

The deterministic survival/fecundity growth rate  $\lambda_D$  was 1.13. The stochastic survival/fecundity growth rate  $\lambda_S$  was  $1.10 \pm 0.12$  (mean  $\pm$  SD). The observed growth rate ( $\lambda_O$ ) based on the actual number of cougars in the study area was  $0.98 \pm 0.16$ . Both of our modeled growth rates were significantly higher than the observed rate (for  $\lambda_D$ ,  $t = 2.09$ ,  $p = 0.05$ ; for  $\lambda_S$ ,  $t = 1.68$ ,  $p = 0.09$ ). Observed growth rates of males ( $\lambda_{OM} = 0.96 \pm 0.15$ ) and females ( $\lambda_{OF} = 0.97 \pm 0.26$ ) were not significantly different ( $t = 0.66$ ,  $p = 0.54$ ). Emigration rates were 0.12 ( $\lambda_O - \lambda_S$ ) and 0.15 ( $\lambda_O - \lambda_D$ ). Observations of radio-collared cougars supported this trend; I documented 5 emigrants and 3 immigrants from 2005 to 2007.

### Population Density

Total maximum cougar density averaged 5.78 animals/100 km<sup>2</sup> and did not change significantly over the study period ( $F = 0.85$ ,  $p = 0.41$ , MS regression  $df = 1$ , MS residual  $df = 4$ ) (Fig. 2). Adult density and adult male density declined (total adults:  $F = 7.09$ ,  $p = 0.06$ , MS regression  $df = 1$ , MS residual  $df = 4$ ; adult males:  $F = 18.92$ ,  $p = 0.01$ , MS regression  $df = 1$ , MS residual  $df = 4$ ). Densities of adult females did not significantly change ( $F = 1.14$ ,  $p = 0.35$ , MS regression  $df = 1$ , MS residual  $df = 4$ ). Average adult density was 3.31/100 km<sup>2</sup>, adult male density was 1.99/100 km<sup>2</sup>, and adult female density was 1.32/100 km<sup>2</sup>.

## Age Structure

Mean age of the population was 41 months (3.4 yrs), mean age of adult males was 60 months (5 yrs), and mean age of adult females was 69 months (5.8 yrs). Mean age of all sex and age classes did not significantly change throughout the study period ( $p > 0.10$ ).

## **DISCUSSION**

Cougar numbers and densities did not increase in response to low hunting mortality. The closed population growth rates from survival and fecundity parameters ( $\lambda_D = 1.13$ ,  $\lambda_S = 1.10$ ) predicted an increasing cougar population, but we did not observe an increase in actual numbers ( $\lambda_O = 0.98$ ). The difference between  $\lambda_D$ ,  $\lambda_S$  and  $\lambda_O$  represents a 12-15 % emigration rate; which was also supported by observations of radio-collared cougars emigrating from the study area. My findings reject the closed population hypothesis and support the open population hypothesis. Compensatory emigration appears to counter high survival/fecundity population growth in this study area. These results are consistent with Robinson et al.'s (2008) findings, whereby compensatory male immigration countered low survival/fecundity population growth in a heavily hunted cougar population.

I may have missed some cougars that were present on the landscape during the study. However, the addition of the same number of cougars each year would not change the observed growth and emigration rates – but simply increase density estimates. A temporal bias such as missing cougars only early in the study (most likely error) would yield an even lower true observed growth rate while missing cougars only later in the

study (least likely error) would yield a higher true observed growth rate. For example, a count of 10 cougars in 2002 and 11 cougars in 2003 would yield an observed growth rate of 1.10. If I missed 3 cougars in 2002, the true growth rate would have been 11/13, or 0.85. I have neither reason nor evidence to suspect that I missed more cougars as the study progressed.

The high emigration rate, comparable growth rates for males and females, and older ages of animals indicate that this population is stable. A younger age structure is characteristic of heavily hunted populations (Logan et al. 1986, Logan and Swenar 2001, Anderson and Lindzey 2005) and may be indicative of a sink population where young males immigrate into available space (Robinson et al. 2008). Stoner et al. (2006) documented significantly lower ages in a heavily hunted population than in an unhunted population (mean adult age of 40.8 months (3.4 yrs) in the hunted area and 55.2 months (4.6 yrs) in the unhunted area). Robinson et al. (2008) also reported significantly ( $p < 0.05$ ) lower mean ages of adult females (46 months, 3.8 yrs) and adult males (41 months, 3.4 yrs) in a heavily hunted population, compared to a mean age of 69 months (5.8 yrs) for adult females and 60 months (5 yrs) for adult males in this study. The relatively low hunting mortality ( $0.11 \pm 0.04$ ) in this study compared to  $0.24 \pm 0.07$  in northern Washington reported by Robinson et al. (2008) did not result in increased numbers and densities of cougars as might be expected.

The older age structure of resident animals in this population may limit immigration and enhance emigration of younger animals. This net emigration response, along with a positive stochastic growth rate, indicates that the population may be self-sustaining and may serve as a population source to the region (Thomas and Kunin 1999).

Source emigration is a stabilizing force among metapopulations, can help sustain sink populations, and may contribute to an increase in the regional growth rate (Pulliam 1988).

The high rates of emigration also indicate that social structure may not impose a ceiling on cougar densities. Early researchers concluded that cougar densities were set via a land tenure social structure (Hornocker 1969, 1970, Seidensticker et al. 1973), whereas more recently Logan and Sweanor (2001) and Pierce et al. (2000) concluded that cougar densities were limited by food supply. I suggest that a combination of both factors may regulate cougar populations. Adequate prey are necessary to support a cougar population, and may dictate initial numbers of cougars on the landscape, but social structure may set ultimate cougar numbers at a lower level than what could be supported by prey as suggested by a type-3 numerical response (Sinclair et al. 2006).

### Management Implications

My findings suggest that emigration counters high survival/fecundity population growth in this lightly hunted cougar population. Low hunting mortality (0.11) did not result in increased numbers and densities of cougars (this study) and high hunting mortality (0.24) did not result in decreased numbers and densities of cougars (Robinson et al. 2008) because of compensatory emigration and immigration responses. Cougar populations appear to be self-regulating in both the absence and presence of high hunting mortality, at least at the smaller game management unit scales ( $< 1,000 \text{ km}^2$ ) observed in these studies, and where prey density is adequate (Pierce et al. 2000). Very heavy hunting (mortality rate = 0.38) at a very large scale ( $10,000 - 30,000 \text{ km}^2$ ) did cause a

cougar population decline, probably because of lack of surviving emigrants in the entire region (Lambert et al. 2006). Heavy hunting at all scales resulted in initial male population increase, a younger age structure, and eventual female population decline (Lambert et al. 2004, Robinson et al. 2008).

Heavy hunting on small scale management units ( $< 1000 \text{ km}^2$ ) does not appear to correspond with decreased cougar numbers and densities (Robinson et al. 2008), and low harvest rates do not correspond with increased cougar numbers and densities as observed during this study. Immigration and emigration countered the population declines and increases predicted by the closed population hypothesis. Managers should incorporate rates of immigration and emigration in addition to survival and fecundity when developing harvest models for cougars and other large carnivores that exhibit open population structure.

## LITERATURE CITED

- Akcakaya, H. R. 2002. RAMAS GIS: Linking spatial data with population viability analysis. Version 4.0. Applied Biomathematics, Setauket, New York, 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.
- Bailey, R. G.; Avers, P. E.; King, T.; McNab, W. H., editors. 1994. Ecoregions and subregions of the United States (map). Washington, DC: USDA Forest Service. 1:7,500,000. With supplementary table of map unit descriptions, compiled and edited by W. H. McNab and R. G. Bailey.
- Beier, P. 1991. Cougar attacks on humans in the United States and Canada. *Wildlife Society Bulletin* 19:403-412
- Bolen, E.G., and W.L. Robinson. 2003. *Wildlife ecology and management*. 5<sup>th</sup> Edition. Prentice Hall. Upper Saddle River, New Jersey, USA.
- Case, T. J. 2000. *An illustrated guide to theoretical ecology*. Oxford University Press, New York, New York, USA.
- Chepko-Sade, B. D. and Z. T. Halpin. 1987. *Mammalian dispersal patterns: the effects of social structure on population genetics*. University of Chicago Press. Chicago, Illinois, USA.
- Cougar Management Guidelines Working Group. 2005. *Cougar management guidelines*. First Edition. Wildfutures, Bainbridge Island, Washington, USA.
- Ebert, T.A. 1999. *Plant and animal methods in demography*. Academic Press, San Diego, California, USA.

- Frank, L. G. and R. Woodroffe. 2001. Behaviour of carnivores in exploited and controlled populations. Pages 419-442 in J. L. Gittleman, S. M. Funk, D. M. Macdonald, and R. K. Wayne, editors. *Carnivore conservation*. Cambridge University Press, Cambridge, UK.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668-674.
- Hornocker, M.G. 1969. Winter territoriality in mountain lions. *Journal of Wildlife Management* 33:457-464.
- Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 21. The Wildlife Society, Lawrence, Kansas, USA.
- Howe, R. W., G. J. Davis and V. Mosca. 1991. The demographic significance of sink populations. *Biological Conservation* 57:239-255.
- Lambert, C. M., R. B. Wielgus, H. S. Robinson, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. *Journal of Wildlife Management* 70:246-254.
- Laundre, J. and T.W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation* 6:159-170.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183-212.
- Logan, K.A., L.L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. *Journal of Wildlife Management* 50:648-654.

- Logan, K.A. and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C., USA.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- Morris, W.F., and D.D. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts USA.
- Murray, D. L. 2007. On improving telemetry-based survival estimation. *Journal of Wildlife Management* 70:1530-1543.
- Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications* 16:1516-1528.
- Pierce, B.M., V.C. Bleich, and R.T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? *Ecology* 81:1533-1543.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- 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.
- Seidensticker, J.C., M.G. Hornocker, W.V. Wiles, and J.P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* 35:1-60.

- Sinclair, A.R.E., J.M. Fryxell, and G. Caughley. 2006. Wildlife ecology, conservation, and management. 2<sup>nd</sup> Edition. Blackwell Publishing, Malden, Massachusetts, USA.
- 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., 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.
- Strickland, M. D., H. J. Harju, K. R. McCaffery, H. W. Miller, L. M. Smith, and R. J. Stoll. 1994. Harvest Management. Pages 445-473 *in* T. A. Bookout editor. Research and Management Techniques for Wildlife and Habitats. The Wildlife Society, Bethesda, Maryland, USA.
- Sweaner, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798-808.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68:647-657.
- 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. and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491-1499.

- Whitman, K.L., A.M. Starfield, H. Quadling, and C. Packer. 2007. Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology* 21:591-601.
- Winterstein, S.R., K.H. Pollock, and C.M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages 35-380 *in* J.J. Millspaugh and J.M. Marzluff editors. *Radio Tracking and Animal Population*. Academic Press. San Diego, California, USA.
- Zar, J. H. 1999. *Biostatistical analysis*. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Zimmerman, F., C. Breitenmoser-Wursten, and U. Breitenmoser. 2005. Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. *Journal of Zoology* 267:381-395.

Figure 1.1. Cle Elum study area. Inset map shows Cougar Management Units (CMU) in Washington. The study area is located along the boundary (Interstate 90) between CMU-5 East Cascades North and CMU-6 East Cascades South.

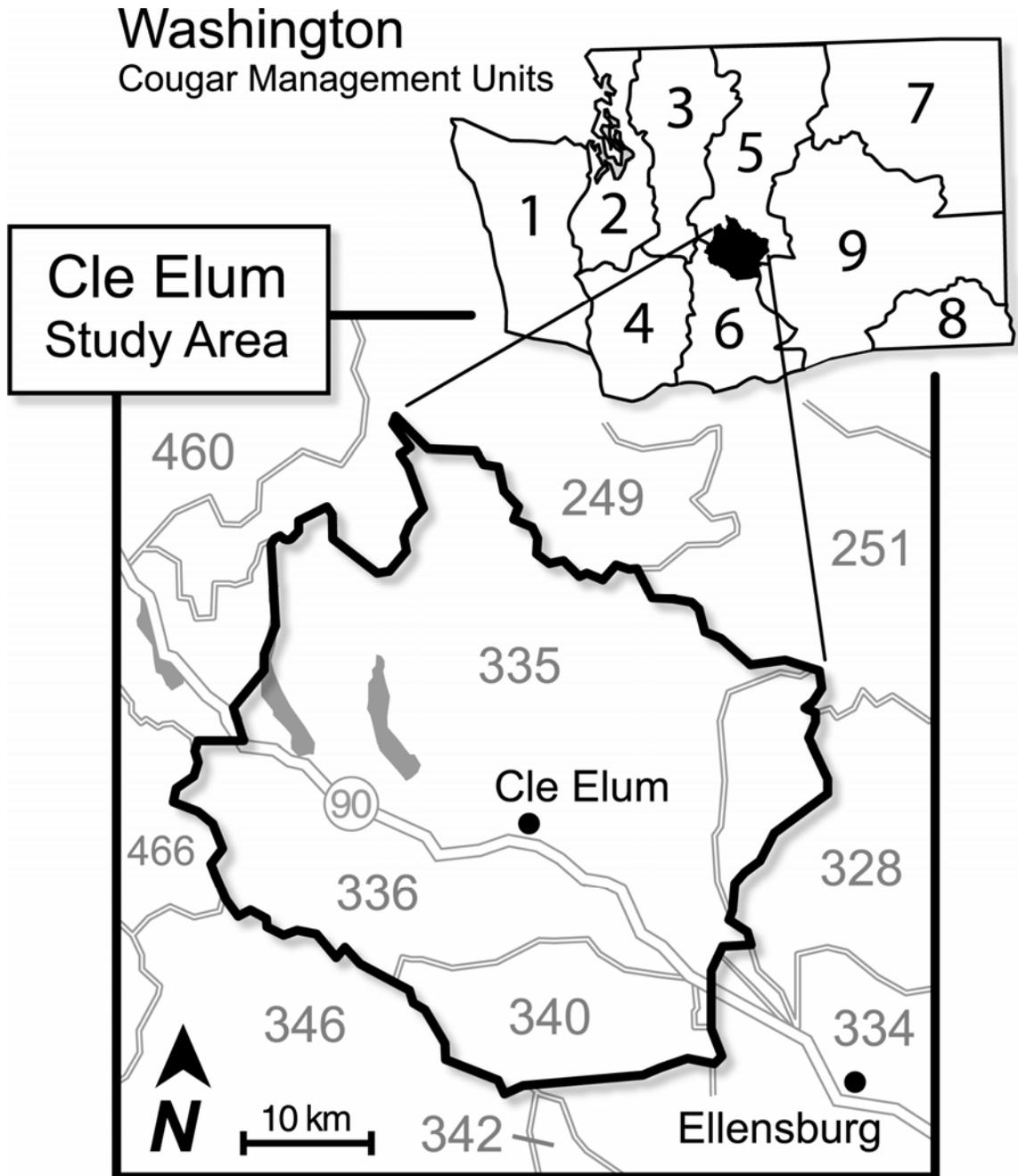


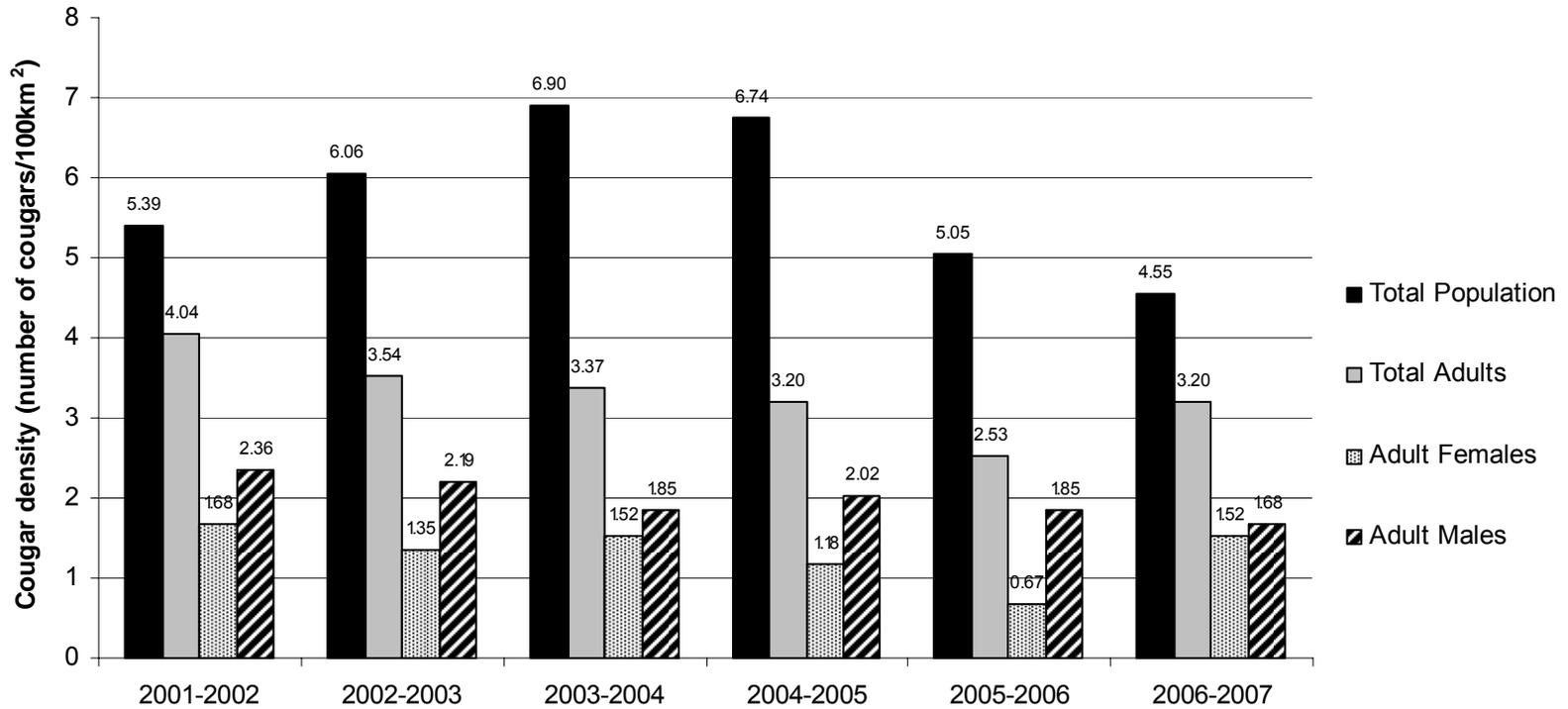
Table 1.1. Mortality rates (mean  $\pm$  SD) and sample sizes (number of dead animals in parentheses) of radio-collared cougars near Cle Elum, Washington, 2002-2007.

Sex and age class	Mortality Source			
	n	Hunting	Vehicle	Natural
<b>Female</b>				
Kitten (0-12 months)	6			0.28 $\pm$ 0.24 (1)
Juvenile (13-24 months)	5	0.24 $\pm$ 0.21 (1)		
Adult (25 + months)	12	0.04 $\pm$ 0.04 (1)		0.09 $\pm$ 0.06 (2)
Female Total	23	0.07 $\pm$ 0.05 (2)		0.10 $\pm$ 0.05 (3)
<b>Male</b>				
Kitten (0-12 months)	13			0.47 $\pm$ 0.17 (4)
Juvenile (13-24 months)	8	0.25 $\pm$ 0.22 (1)	0.25 $\pm$ 0.22 (1)	
Adult (25 + months)	12	0.20 $\pm$ 0.09 (4)	0.10 $\pm$ 0.07 (2)	0.05 $\pm$ 0.05 (1)
Male Total	33	0.16 $\pm$ 0.06 (5)	0.09 $\pm$ 0.05 (3)	0.16 $\pm$ 0.06 (5)
Population Total	56	0.11 $\pm$ 0.04 (7)	0.05 $\pm$ 0.03 (3)	0.13 $\pm$ 0.04 (8)

Table 1.2. Radio-days, sample size (number of mortalities with total number of monitored animals in parentheses), and survival rates (mean  $\pm$  SD) by sex and age class for radio-collared cougars near Cle Elum, Washington, 2002-2007.

<b>Age Class</b>	<b>Females</b>			<b>Males</b>		
	<b>Radio days</b>	<b>n</b>	<b>Survival rate</b>	<b>Radio days</b>	<b>n</b>	<b>Survival rate</b>
<b>Kitten (0-12 months)</b>	1094	1 (6)	0.7162 $\pm$ 0.24	2295	4 (13)	0.5290 $\pm$ 0.17
<b>Juvenile (13-24 months)</b>	1310	1 (5)	0.7567 $\pm$ 0.21	1084	2 (8)	0.5095 $\pm$ 0.24
<b>Adult (25 + months)</b>	7601	3 (12)	0.8658 $\pm$ 0.07	5851	7 (12)	0.6461 $\pm$ 0.11
<b>Total (all ages)</b>	10005	5 (23)	0.8332 $\pm$ 0.07	9230	13 (33)	0.5978 $\pm$ 0.08

Fig.1.2. Total and adult cougar (>24 months old) densities near Cle Elum, Washington, 2002 - 2007.



**CHAPTER TWO**

**DOES HUNTING REGULATE COUGAR POPULATIONS? A TEST OF THE  
COMPENSATORY MORTALITY HYPOTHESIS**

## **ABSTRACT**

Many wildlife species are managed based on the Compensatory Mortality Hypothesis (CMH), which predicts that harvest mortality (especially adult male mortality) will trigger density-dependent responses in reproduction, survival, and population growth caused by reduced competition for resources. I tested the CMH on two cougar populations (one heavily hunted and one lightly hunted) in Washington. I estimated population growth, density, survival, and reproduction to determine effects of hunting on cougar population demography based on data collected from 2002-2007. The heavily hunted population had an overall hunting mortality rate of 0.24 and 0.46 for males. The lightly hunted population had an overall mortality rate of 0.11 and 0.20 for males. The CMH predicts that higher overall and adult male hunting mortality will result in higher maternity, kitten survival, reproductive success, and lower natural mortality of adult females. I found no differences in rates of maternity or natural mortality. Kitten survival was lower in the heavily hunted population. I rejected the CMH because vital rates did not compensate for hunting mortality. Heavy harvest corresponded with immigration, reduced kitten survival, reduced female population growth, and a younger overall age structure. Light harvest corresponded with emigration, higher kitten survival, increased female population growth, and an older overall age structure. Managers should account for dispersal, survival, and fecundity when developing harvest prescriptions for cougars.

## INTRODUCTION

Density-dependent population regulation has been experimentally demonstrated for a variety of animals and forms the theoretical basis for sustainable hunting of polygynous mammals (Caughley, 1977; Caughley and Sinclair, 1994; Ginsburg and Milner-Gulland, 1994; Strickland et al., 1994). The compensatory mortality hypothesis (CMH) predicts that harvest mortality, especially of surplus adult males, triggers density-dependent responses in reproduction, offspring survival, and female population growth by reducing competition for resources (Connell, 1978). In unharvested or lightly harvested populations, higher densities generate increased competition for resources, and subsequently decreased reproduction, offspring survival and female population growth. Therefore, removal of surplus adult males in polygynous mating systems is generally considered to have benign or beneficial effects on population growth (Errington, 1945; Johnson et al., 2001; Frank and Woodroffe, 2001).

The CMH model of population growth has been demonstrated for a variety of ungulates (Staines, 1978; Burnham and Anderson, 1984; Peek, 1986; Bartmann et al., 1992; White and Bartmann, 1988), but little evidence suggests that the model fits carnivore populations (Franke and Woodroffe, 2001; Milner et al., 2007). Because life histories of carnivores and ungulates differ, I would also expect that density dependence might operate differently. Ungulates typically have restrictive or limited dispersal movements compared to carnivores (Chepko-Sade and Halpin, 1987; Howe et al., 1991; Franke and Woodroffe, 2001; Zimmerman et al., 2005; Whitman et al., 2007). Therefore hunting surplus males is likely to reduce local herbivore densities but might not have the same effect on carnivores. Such intrinsic emigration can depress population density, and

intrinsic immigration can increase population density regardless of birth and death rates (Franke and Woodroffe, 2001; Festa-Bianchet, 2003). This exchange of animals via immigration and emigration may offset expected changes in density and associated effects on vital rates of resident female animals. As a result, harvest levels that are considered beneficial or benign to an ungulate population may impose additive mortality on carnivores (Franke and Woodroffe, 2001; Festa-Bianchet, 2003; Swenson, 2003).

Cougars are managed for sport harvest and population control based on the CMH throughout the western U.S. (Cougar Management Guidelines Working Group, 2005:71-82; Strickland et al., 1994). Managers seeking to provide trophy hunting opportunities often adopt strategies that seek to reduce male densities (“surplus males”) and keep female numbers high (Hemker et al., 1984; Ross and Jalkotzy, 1992; Lindzey et al., 1994; Spreadbury et al., 1996; Logan and Sweanor, 2001; Martorello and Beausoleil, 2003). However, young male cougars often disperse long-distances. Harvesting of adult males can create vacancies that attract these young dispersers to vacated territories (Hemker et al., 1984; Logan et al., 1986; Ross and Jakotzy, 1992; Logan and Sweanor, 2001; Stoner et al., 2006; Robinson et al., 2008). Robinson et al. (2008) showed that heavy hunting pressure on cougars did not reduce the population in a small scale management area, because of compensatory immigration. Their results suggest that density-dependence in cougar populations may act through dispersal and that CMH-based models of cougar management may be inappropriate.

I tested the CMH of hunting on two Washington cougar populations (one heavily hunted and one lightly hunted) from 2002-2007. The CMH predicts that heavy hunting of cougars will result in 1) decreased male densities, 2) increased maternity rates, 3)

increased survival of young, 4) decreased natural mortality, and 5) increased female population growth; and that low levels of harvest of cougars will result in 1) increased male densities, 2) decreased maternity rates, 3) decreased survival of young, 4) higher natural mortality rates, and 5) decreased female population growth.

## **STUDY AREAS**

I monitored cougar population in two study areas > 250 km apart and managed under different hunting strategies. Heavy hunting with the aid of hounds (hunting mortality rate = 0.24) was permitted in the Northeast Washington area and light hunting without the use of hounds (hunting mortality rate = 0.11) was permitted in the Central Washington study area.

### Northeast Area

The 735 km<sup>2</sup> study area lies north of the town of Kettle Falls, and includes a patchwork of federal, state, and privately owned lands. The study area is bounded on the southeast and southwest by the Columbia and Kettle Rivers. The Canadian-United States border forms the northern boundary. The area is part of a glacially subdued mountainous region (400-2,130 m elevation) known as the Okanogan Highlands, and occupies the transition between the East-slope Cascades and Northern Rocky Mountain physiographic province (Bailey et al., 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the 46 cm annual precipitation falls as snow with an average of 136 cm falling from mid-November to mid-

April annually. Mean annual temperatures ranges from  $-6^{\circ}\text{C}$  in January to  $21^{\circ}\text{C}$  in July. White-tailed deer (*Odocoileus virginianus*) are the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) are also present. Common predator species besides cougar include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*).

### Central Area

The study area is located along the east slope foothills of the North Cascades Mountains near the town of Cle Elum. The area covers  $594\text{ km}^2$  and includes a portion of the upper Yakima River watershed. The Cascade Mountains form the western boundary, the Enchantment Wilderness forms the north and unforested agricultural lands of the Kittitas Valley form the south and east. Sagebrush steppe foothills (below 550 m elevation) transition upwards to ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) covered slopes. Sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) dominate ridges at elevations  $> 1550\text{ m}$ . Precipitation averages  $56.4\text{ cm/yr}$ , with  $160\text{ cm}$  of snowfall during winter). Mean annual temperature ranges from  $-7^{\circ}\text{C}$  in January to  $27^{\circ}\text{C}$  in July. Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species besides cougar include coyotes, black bears, and bobcats.

## **METHODS**

### Captures and Monitoring

I attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of each study area during winter when tracks are detected in snow. I used hounds to track and tree cougars in winter (Hornocker, 1970). I immobilized treed cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 mL/10 kg of body mass, or with Telazol at a dosage of 6 mg/kg, using a projectile dart in the hindquarter (Ross and Jalkotzy, 1992; Spreadbury et al., 1996). I determined sex and classified animals as kittens (0-12 months), juveniles (13-24 months), or adults (25+ months) based on physical measurements and gum regression measurements of the canine teeth (Laundre et al., 2000).

I fitted each animal with a mortality-sensing Very High Frequency (VHF, Advanced Telemetry Systems, Isanti MN) or Global Positioning System (GPS, Lotek Wireless Inc, Newmarket, Ontario and Televilt, Lindesberg, Sweden) collar. Beginning in January 2005, I investigated den sites of collared females, and captured kittens by hand. I collared kittens that were >6-weeks old with expandable VHF (Telonics Inc, Mesa, AZ; T. Ruth personal communication 2004) radio collars to accommodate growth (Telonics Inc, Mesa, AZ; T. Ruth design 2004). I handled all animals in accordance with Washington State University Animal Care (IACUC Permit #3133) and Animal Welfare Assurance Committee (AWAC Permit #A3485-01). GPS collars were programmed to collect locations at 4 hour intervals (6 times/day). The data were retrieved using a remote

communication unit. I recorded location coordinates of VHF-collared animals at one-week intervals from ground or aerial telemetry.

Despite attempts to systematically search and mark animals, I was not able to mark the entire population. Therefore, to establish a minimum population estimate for each study area I included demographic data from collared and uncollared cougars that were harvested by hunters, killed during depredation hunts, and killed by vehicle collisions (Stoner et al. 2006, Robinson et al. 2008). Washington Department of Fish and Wildlife recorded sex and age (determined by cementum annuli) for uncollared cougars killed by hunters or killed by special harvest permits or other causes. Because measurements of gum regression and cementum annuli yield comparable ages (Robinson et al., 2008), I included all collared and uncollared animals in a linear regression analysis to examine trends in age structure over the study period.

### Survival

I used radio-telemetry to monitor survival of all radio-collared cougars and assigned cause of mortality as hunting, vehicle, or natural. Natural mortalities were confirmed with necropsies. I inferred cause of kitten mortalities by examining the carcass and proximity to collared cougars.

I used the modified Mayfield method (Heisey and Fuller, 1985) to estimate survival of animals because it provides increased precision when mortality rates are high, performs well in the case of small sample size typical of large carnivore species, and can identify cause-specific mortality rates (Winterstein et al., 2001; Murray, 2007). I

calculated annual survival rates for male and female kittens, juveniles, and adults from January 2002 to December 2007.

To determine intervals when survival probabilities were constant I analyzed the statistical distribution of deaths over a 365-day period (Lambert et al., 2006). This yielded two seasons: a high (Central: 1 Aug to 31 Dec, Northeast: 1 Oct to 31 Jan) and a low mortality season (Central: 1 Jan to 31 July, Northeast: 2 Feb to Sept 31). I calculated survival rates for each season and then multiplied them together for an annual rate (Heisey and Fuller, 1985). I chose intervals for each period based on the median date of the deaths for each period. I used the Taylor series approximation method to compute variances of class-specific survival rates, and a one-tailed z-test to determine whether survival rates in Central were higher than in Northeast (Micromort version 1.3, Heisey and Fuller 1985).

### Maternity and fecundity

I calculated maternity as the mean number of kittens observed during inspection of maternal dens and from snow tracking divided by the number of adult females observed that year (Case, 2000:183). I calculated fecundity rates,  $F = S_F \times M_{x+1}$  from the female survival rate in year x multiplied by their mean maternity rate the following year (Ebert, 1999). I used two-tailed t-tests assuming unequal variance to compare maternity and fecundity rates from each area (Zar 1999).

### Deterministic and stochastic growth rates

I constructed a survival/fecundity dual-sex Leslie matrix (Leslie, 1945) to model closed population growth for each area in RAMAS GIS (Akçakaya, 2002a). I also included female age at first reproduction = 24 months, sex ratio at birth = 1:1, and maximum age and age at senescence = 13 years (Robinson et al., 2008).

I calculated the deterministic growth rate ( $\lambda_D$ ) as the dominant eigenvalue of the matrix under a stable age distribution. I calculated the stochastic growth rate ( $\lambda_S$ ) by incorporating annual environmental variability (standard deviation of annual survival and fecundity rates) and demographic stochasticity. To estimate demographic stochasticity, I sampled the number of survivors in each sex and age class from a binomial distribution, and the number of kittens born each year from a Poisson distribution using the random number generator of RAMAS GIS (Akçakaya 2002). I sampled vital rates from a lognormal distribution to avoid truncations, which can occur if standard deviations are large due to sampling and measurement error. I projected each population for six years (five transitions), and calculated  $\lambda_S$  as the average geometric mean growth rate from 200 simulations, the point at which rates converged (Robinson et al. 2008).

### Observed growth, immigration, and emigration

I determined the observed growth rates ( $\lambda_O$ ) from annual counts of collared and unmarked cougars. Each year I tallied the number of cougars (adults, juveniles, and kittens) in each study area and calculated  $\lambda_O$  as  $\lambda_x = (n_t / n_o)^{1/t}$  where  $\lambda_x$  is the annual finite growth rate,  $n_o$  is the starting population,  $n_t$  is the final population, and  $t$  is the number of transitions between the start and end of the population projection (Case 2000).

I used a one-tailed, one-sample t test to determine whether deterministic ( $\lambda_D$ ) and stochastic ( $\lambda_S$ ) growth rates were higher than the average six-year observed ( $\lambda_O$ ) growth rate for Central, and whether  $\lambda_D$  and  $\lambda_S$  were lower than  $\lambda_O$  for Northeast (Zar 1999). I estimated net immigration/emigration rate ( $i/e$ ) using the equations  $i/e = \lambda_D - \lambda_O$  and  $e = \lambda_S - \lambda_O$  (Peery et al., 2006). I also used observations of radio-collared cougars to document emigration and immigration in each area from 2005 through 2007, the period during which I had accurate kitten survival data.

### Population density

I estimated mean annual densities of cougars (cougars/100 km<sup>2</sup>) for each study area as the proportion of male and female locations (McLellen, 1989) that fell inside in the mean annual 95% composite range for females. For unmarked cougars I used the mean proportion of marked animals. I back-calculated the lifespan of each marked and unmarked cougar to the beginning of the study, its birth date, or immigration date as described by Logan and Sweanor (2001:66), Stoner et al. (2006), and Robinson et al. (2008). I used a general linear modeling (GLM) approach to test for independent effects of study area and time on cougar density. I included area, time, time<sup>2</sup>, time x area, and time<sup>2</sup> x area as independent variables and then selected variables stepwise in a backwards fashion, removing those that failed to be significant at the 0.10 significance level (Zar 1999).

### Age Structure

I calculated sex ratios (F:M) from collared cougars only to prevent bias that may result from hunters selecting for male cougars (trophies). I determined whether ratios were different from equality with a Chi-square goodness of fit test (Zar 1999). I compared mean age of cougars in each area with a 2 sample t-test and examined the trend in age structure with simple linear regression (Zar, 1999).

### Confounding Factors

To account for possible differences in per capita resources affecting maternity, kitten survival and female population growth, I compared cougar densities and female kill rates in the two study areas. I compared differences in densities with General Linear Models and tested for differences in kill rates with a two-tailed t-test (Zar 1999).

## **RESULTS**

### Captures and Monitoring

I captured and marked 103 cougars in the 2 study sites (57 in Northeast, 46 in Central) between January 2002 and December 2007. Fifty unmarked cougars were killed by hunters (9 females, 13 males in Northeast; 14 females, 13 males, 1 of unknown sex in Central) and 1 uncollared female in Central was killed by a vehicle collision. Twenty-six unmarked kittens (6 females, 2 males, 9 of unknown sex in Northeast; 3 females, 4 males, 2 of unknown sex in Central) were observed traveling with collared females.

## Survival and Mortality

Fifty-three (35 in Northeast, 18 in Central) radio-collared cougars were killed during the study (Table 2.1). Twenty-six were killed by hunters (19 in Northeast, 7 in Central), 22 died from natural causes (14 in Northeast, 8 in Central), 3 died in vehicle collisions in Central, and 2 were killed from depredation hunts in Northeast. Eight juveniles (2 in Northeast, 6 in Central) emigrated and were censored at the last known date of their location. An additional 9 (4 in Northeast, 5 in Central) animals were censored due to shed collars or lost VHF signals. Of 42 radio-collared kittens (23 in Northeast, 19 in Central), 18 survived to one year of age (6 males, 2 females in Northeast, and 6 males, 4 females in Central), 16 died from natural causes (5 females, 5 males, 1 unknown sex in Northeast, 1 female, 4 males in Central), and 4 were censored (2 females in Northeast, 2 males in Central). Six of the 'natural' kitten mortalities in Northeast were caused male cougars (3 females, 2 males, 1 unknown sex). This was confirmed by canine tooth punctures in the skull (2 kittens) and close proximity of a collared male at estimated time of death (4 kittens).

Average annual survival rates for all radio-collared cougars in Northeast were  $0.56 \pm 0.05$  (SD) and in Central  $0.71 \pm 0.06$ , but survival varied with age and sex classes (Table 2.2). Overall survival and survival of adults was higher in Central than in Northeast (overall:  $Z = 1.98$ ,  $p = 0.02$ ; adults:  $Z = 1.75$ ,  $p = 0.04$ ). Survival of adult females and survival of kittens was also higher in Central (adult females:  $Z = 1.88$ ,  $p = 0.03$ ; kittens:  $Z = 1.49$ ,  $p = 0.07$ ). I did not detect differences among other sex or age comparisons. Survival rates for kittens were  $0.32 \pm 0.11$  in Northeast and  $0.58 \pm 0.14$  in Central, for adult females:  $0.66 \pm 0.08$  in Northeast and  $0.87 \pm 0.07$  in Central, and for

adult males:  $0.48 \pm 0.12$  in Northeast and  $0.65 \pm 0.11$  in Central. I removed six kittens from the analysis that were killed by male cougars in the Northeast, recalculated survival rates, and found that kitten survival was the same ( $Z = 0.96$ ,  $p = 0.96$ ) in Northeast ( $0.59 \pm 0.02$ ) and Central ( $0.58 \pm 0.02$ ). Overall mortality rate from hunting was higher ( $Z = 2.02$ ,  $p = 0.04$ ) in Northeast ( $0.24 \pm 0.05$ ) than in Central ( $0.11 \pm 0.04$ ). I found no differences in natural mortality rates (Northeast =  $0.18 \pm 0.04$ , Central =  $0.13 \pm 0.04$ ;  $Z = 0.77$ ,  $p = 0.44$ ). The standard deviation of annual survival rates for all cougars was 0.09 in Northeast and 0.06 in Central.

#### Maternity and fecundity

Mean litter size was  $2.63 \pm 0.80$  ( $n = 18$  litters) in Northeast and  $2.47 \pm 0.83$  ( $n = 15$  litters) in Central, and did not differ between study areas ( $t = 2.04$ ,  $df = 30$ ,  $p = 0.94$ ). Proportions of females producing newborns (0.44 in Northeast and 0.51 in Central) were not different ( $Z = -0.41$ ,  $p = 0.68$ ), and proportions of females with dependent kittens (0.58 in the Northeast and 0.75 in Central) were also not different ( $Z = 1.15$ ,  $p = 0.25$ ). Mean maternity in the Northeast (1.15 kittens/female/year) did not differ from Central (1.12 kittens/female/year;  $t = 2.26$ ,  $df = 9$ ,  $p = 0.94$ ). Fecundity rates in the Northeast ( $0.76 \pm 0.63$ ) also did not differ from Central ( $0.97 \pm 0.38$ ;  $t = 2.31$ ,  $df = 8$ ,  $p = 0.49$ ). The standard deviation of annual fecundity rates was 0.25 in the Northeast and 0.27 in the Central area.

### Population Growth

The deterministic annual female growth rates ( $\lambda_D$ ) based on survival and fecundity models were 0.80 in Northeast and 1.13 in Central. The stochastic growth rate (mean  $\lambda_S \pm$  SD) for Northeast ( $0.78 \pm 0.19$ ) was lower than in Central ( $1.10 \pm 0.12$ ,  $t = 21.09$ ,  $p < 0.01$ ). The observed growth rates ( $\lambda_O$ ) based on the actual number of cougars in the study area were 0.91 (female  $\lambda_O = 0.86$ , male  $\lambda_O = 1.02$ ) for the Northeast and 0.98 (female  $\lambda_O = 0.97$ , male  $\lambda_O = 0.96$ ) for Central, and were not different ( $t = 0.86$ ,  $p = 0.42$ ). Modeled growth rates were significantly higher than  $\lambda_O$  in Central (for  $\lambda_D$ ,  $t = 2.09$ ,  $p = 0.05$ ; for  $\lambda_S$ ,  $t = 1.68$ ,  $p = 0.09$ ) and lower than  $\lambda_O$  in Northeast (for  $\lambda_D$ ,  $t = 2.10$ ,  $p = 0.07$ ; for  $\lambda_S$ ,  $t = 2.46$ ,  $p = 0.05$ ). The Northeast population had a net immigration rate of 0.11 ( $\lambda_O - \lambda_D$ ) and 0.13 ( $\lambda_O - \lambda_S$ ), and the Central population had a net emigration rate of 0.12 ( $\lambda_O - \lambda_S$ ) and 0.15 ( $\lambda_O - \lambda_D$ ). Observations of radio-collared cougars supported these trends; I documented 5 emigrants and 3 immigrants in Central, and 4 immigrants and 0 emigrants in Northeast from 2005 through 2007.

### Population Density

The mean 95% composite range of females was 772 km<sup>2</sup> (95% CI = 316 – 1228) for Northeast and 655 km<sup>2</sup> (95% CI = 425 – 885) for Central. The mean ( $\pm$  SD) annual proportion of male GPS points within the composite range of females was  $0.32 \pm 0.08$  in Northeast and  $0.43 \pm 0.16$  in Central.

Time and time x area explained significant variation in cougar density ( $p < 0.10$ ). I left area in the model because it was a variable of interest. The final model included: area, time, and time x area. Mean annual densities of all cougars were  $3.46 \pm 0.69/100$

km<sup>2</sup> in Northeast and  $3.62 \pm 0.58/100$  km<sup>2</sup> in Central, and were not different (Tables 2.3, 2.4). Densities of males and females were lower in Northeast (males:  $0.63 \pm 0.12$  Northeast vs.  $1.30 \pm 0.15/100$  km<sup>2</sup> in Central, females:  $2.83 \pm 0.76$  in Northeast vs.  $2.32 \pm 0.44$  in Central). In the Northeast, densities of all cougars and females declined over the study period, whereas I detected no change in male densities. In Central WA, I also did not detect a change in density for any sex and age class (all  $p > 0.05$ , Table 2.4).

### Sex & Age Structure

Mean age of the Northeast cougar population was 27 months (2.3 yrs) and 38 months (3.2 yrs) in Central WA (Table 2.3). Mean ages of cougars in Central were higher than in the Northeast for all age and sex classes (all  $p < 0.05$ ) except for mean age of females ( $p = 0.10$ ) (Table 2.3). Mean age of female cougars in Northeast increased ( $P < 0.05$ ) and I did not detect a change in male densities ( $p > 0.10$ ). I detected no changes in age for Central ( $p > 0.10$ ).

### Confounding Factors

I found no differences in mean maternity rates ( $t = 2.26$ ,  $df = 9$ ,  $p = 0.94$ ), kill rates ( $t = 0.79$ ,  $df = 34$ ,  $p = 0.44$ ), or population density ( $t = 1.47$ ,  $df = 1$ ,  $p = 0.26$ ) between areas. The female kill rate in Northeast was 6.68 days/kill (Cooley et al. 2008) and 7.04 days/kill in Central (K. White unpublished data, 2008).

## **DISCUSSION**

Data comparing demographics of 2 Washington cougar populations suggest that hunting does not act in a compensatory manner in cougar populations. The Compensatory Mortality Hypothesis (CMH) predicts that increased harvest mortality of males will reduce population density, resulting in lower competition for resources, reduced natural mortality, and increased reproduction and survival of young. CMH predicted that low levels of harvest will result in increased densities and rates of natural mortality, and decreased reproduction and survival. However, in the heavily hunted area, male densities remained unchanged because of immigration and female densities declined, whereas in the lightly hunted area, I observed no change in male or female densities. I found no differences in rates of natural mortality (0.18 in Northeast and 0.13 in Central) or maternity rates (1.15 Northeast vs. 1.12 in Central). Kitten survival was lower in the heavily hunted Northeast (0.32 in Northeast WA and 0.58 in Central) with none of the kitten mortalities from hunting or to death of the mother. Female population growth was negative in Northeast and stable in Central. My findings reject the Compensatory Mortality Hypothesis because vital rates did not compensate for hunting mortality.

Resource availability could have influenced vital rates; however both populations were at similar densities (3.46 cougars/100km<sup>2</sup> in Northeast and 3.62 cougars/100km<sup>2</sup> in Central) and female predation rates were not different, suggesting that resources were equal between areas. Densities were maintained via a net immigration rate in Northeast and a net emigration in Central. The net emigration rate in Central could indicate poorer resources, but kitten survival and female population growth were higher there. The net

immigration rate in Northeast suggests better resources, but kitten survival and female population growth were lower there.

Instead of influencing survival and reproduction, effects of hunting were compensated for through immigration and emigration in both cougar populations. The stochastic population model, based on the CMH, predicted a 27% population decline in response to heavy harvest in the Northeast, whereas I observed only a 9% decline in overall numbers and no decline in the male population. The difference in growth rates was caused by model structure; the stochastic model assumed a closed population structure and did not account for immigration and emigration, whereas the observed growth rate accounted for the open nature of cougar populations by including immigration and emigration. The majority of animals removed through hunting were replaced by animals immigrating from neighboring area. In the lightly-hunted population, the stochastic model predicted a 10% increase in population growth, yet cougar numbers remained stable. The projected population increase was compensated for by emigration rather than by decreased vital rates. Therefore, neither population density nor competition among cougars was changed by hunting, but immigration and emigration counteracted the effects predicted by the CMH. Long-distance dispersal is common in cougars (Sweaner et al., 2000; Logan and Sweaner, 2001; Stoner et al., 2006; Robinson et al., 2008) and can promote population persistence and recovery by replacing harvested animals with dispersers from neighboring areas (Hanski, 2001). Recovery from heavy hunter harvest by immigration has been documented in several cougar populations (Ross and Jalkotzy, 1992; Logan et al., 1996; Logan and Sweaner, 2001; Anderson and Lindzey, 2005; Stoner et al., 2006; Robinson et al., 2008). As a consequence, harvest

models based on CMH are unable to accurately predict the population responses to hunting.

The Northeast population compensated for heavy harvest in overall numbers of cougars through male immigration. However, the female population declined. Whereas male cougars commonly disperse long distances, females frequently are philopatric (Sweanor et al., 2000). As a result, fewer female immigrants are available to replace those that are harvested, and numbers of females decrease. Adult female survival is vital for population growth and recovery from harvest (Martorello and Beausoleil, 2003).

Harvesting adult males may increase incidences of infanticide by allowing immigration of new, unrelated males (Ross and Jalkotzy, 1992; Whitman and Packer, 1998; Murphy et al., 1999; Logan and Sweanor, 2001). Lower kitten survival in Northeast may have been a result of high male turnover caused by hunting. Male carnivores have been known to kill unrelated young in order to induce estrous and gain breeding opportunities (Packer and Pusey, 1983; Wielgus and Bunell, 1985; Smith and McDougal, 1991; Swenson, 1997; Logan and Sweanor, 2001). Field evidence suggests that 6 kittens in 3 litters in the Northeast were killed by unrelated male cougars. When I removed those 6 kittens from the survival analysis, I found no difference in survival rates of kittens between areas, suggesting that infanticide may have been responsible for lower kitten survival in the heavily hunted area.

Regulatory mechanisms of cougar populations have been debated for many years. Early studies concluded that densities were set intrinsically, via a tenure-based social structure (Hornocker, 1970; Seidensticker et al., 1973). More recent studies have concluded that densities are regulated extrinsically, by food supply (Logan and Sweanor,

2001; Pierce et al., 2000). My data suggests an alternative hypothesis: cougar populations self-regulate through dispersal. Wolff (1997) defines self-regulation as any “intrinsic behavioural mechanism that prevents or retards population growth prior to the population reaching food limitation”. Emigration prevented the Central population from increasing and immigration prevented the Northeast from a severe population decline. Although I have no measure of prey density to detect food limitation, I did not observe any evidence of starvation, and predation rates were consistent across the study period (K. White, unpublished data 2008, J. Keehner, unpublished data 2008, Cooley et al. 2008). I am not suggesting that food supply and cougar densities are independent, rather that dispersal exerts a stronger influence on the population than food supply at the prey densities observed in my study areas. High rates of immigration following heavy male harvest were also observed in brown bears (*Ursus arctos*) (Wielgus and Bunnell, 1994) and black bears (*Ursus americanus*) (Sargeant et al. 2001). Female population growth declined because of sexually selected infanticide in brown bears (Wielgus and Bunnell, 1994; Swenson, 1997). This may indicate that the CMH approach to harvest is inaccurate for many solitary, territorial, or quasi-territorial carnivores.

I may have missed some cougars that were present on the landscape during the study. However, the addition of the same number of cougars each year would not change the observed growth and emigration rates – but simply increase density estimates. A temporal bias such as missing cougars only early in the study (most likely error) would yield an even lower true observed growth rate while missing cougars only later in the study (least likely error) would yield a higher true observed growth rate. For example, a count of 10 cougars in 2002 and 11 cougars in 2003 would yield an observed growth rate

of 1.10. If I missed 3 cougars in 2002, the true growth rate would have been 11/13, or 0.85. I have neither reason nor evidence to suspect that I missed more cougars as the study progressed.

## **CONSERVATION IMPLICATIONS**

Harvest models that are based on the CMH approach rely on the assumption that hunting reduces densities. However, my results suggest that dispersal movements may counteract population decreases caused by hunting. These findings have two management implications: 1) recovery from harvest relies on nearby source populations, therefore cougar harvest should be managed at the metapopulation scale (Cougar Management Guidelines Working Group, 2005:73-74), and 2) even when healthy source populations exist, prolonged harvest will cause female population declines, a younger age structure to develop, and increased kitten mortality caused by immigration of potentially infanticidal males (Ross and Jalkotzy, 1992; Logan and Sweanor, 2001, this study), and kitten abandonment from harvest of mothers (R. Beausoleil, personal communication 2008). Managers need to account for dispersal in addition to survival and fecundity when developing hunter harvest models and prescriptions for cougars, and other large carnivores that exhibit long-distance dispersal, because assumptions of closed populations are not appropriate for these species.

## LITERATURE CITED

- Akçakaya H.R., 1991. A method for simulating demographic stochasticity. *Ecological Modelling* 54, 133–136.
- Akçakaya H.R., 2002a. RAMAS Metapopulations: viability analysis for stage-structured metapopulations. Version 4.0. Applied Biomathematics. Setauket, New York, USA.
- Akçakaya H.R., 2002b. Estimating the variance of survival rates and fecundities. *Animal Conservation* 5, 333–336.
- Anderson, C.R., Jr., Lindzey, F.G., 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. *Wildlife Society Bulletin* 33, 179-188.
- Bailey, R. G.; Avers, P. E.; King, T.; McNab, W. H., (Eds.), 1994. Ecoregions and subregions of the United States (map). Washington, DC: USDA Forest Service. 1:7,500,000.
- Bartmann, R.M., White, G.C., Carpenter, L.H., 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs* 121, 1-39.
- Boyce, M.S., Sinclair, A.R.E., White, G.C., 1999. Seasonal compensation of predation and harvesting *Oikos* 87, 419-426.
- Burnham, K.P., Anderson, D.R., 1984. Tests of compensatory vs. additive hypothesis of mortality in mallards. *Ecology* 65, 105-112.
- Caswell H., 2001. Matrix population models: construction, analysis, and interpretation. Sinauer.
- Caughley, G., 1977. Analysis of vertebrate population. Wiley & Sons.

- Caughley, G., Sinclair, J., 1994. *Wildlife Ecology and Management*. Blackwell Science.
- Chepko-Sade, B. D., Halpin, Z.T., 1987. *Mammalian dispersal patterns: the effects of social structure on population genetics*. University of Chicago Press.
- Clutton-Borck, T.H., Major, M., Albon, S.D., Guinness, F.E., 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology* 56, 53-67.
- Cooley, H.S., Wielgus, R.B., Robinson, H.S., and Lamert, C.S. 2008. Cougar prey selection in a white-tailed deer and mule deer community. *Journal of Wildlife Management* 72:99-106.
- Dhondt, A.A., Kempenaers, B., Adriaensen, F., 1992. Density-dependent clutch size cause by habitat heterogeneity. *Journal of Animal Ecology* 61, 643-648.
- Douglas, C.L., Leslie, D.M., 1986. Influence of weather and density on lamb survival of desert mountain sheep. *Journal of Wildlife Management* 50:153-156.
- Errington, P.L., 1945. Some contributions of a fifteen-year study of the northern bobwhite to a knowledge of population phenomena. *Ecological Monographs* 15, 1-34.
- Festa-Bianchet, M., 2003. Exploitative wildlife management as a selective pressure for life-history evolution of large mammals. In: Festa-Bianchet, M., Apollonio, M. (Eds.), *Animal Behavior and Wildlife Conservation*. Island Press.
- Fowler, C.W., Smith, T.B., 1981. *Dynamics of large mammal populations*. Wiley & Sons.

- Frank, L. G., Woodroffe, R., 2001. Behaviour of carnivores in exploited and controlled populations. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K. (Eds.), *Carnivore conservation*. Cambridge University Press, pp. 419-442.
- Ginsberg, J.R., Milner-Gulland, E.J., 1994. Sex-biased harvesting and population dynamics: Implications for conservation and sustainable use. *Conservation Biology* 8, 157-166.
- Hanski, I., 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. In: Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Eds.), *Dispersal*. Oxford University Press.
- Hemker, T.P., Lindzey, F.G., Ackerman, B.B., 1984. Population characteristics and movement patterns of cougars in southern Utah. *Journal of Wildlife Management* 48, 1275-1284.
- Hornocker, M.G., 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 21, 1-39.
- Howe, R. W., Davis, G.J., Mosca, V., 1991. The demographic significance of sink populations. *Biological Conservation* 57, 239-255.
- Johnson, W.E., Eizirik, E., Lento, G., 2001. The control, exploitation, and conservation of carnivores. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K. (Eds.), *Carnivore Conservation*. Cambridge University Press, pp.196-220.
- Lack, D. 1954., *The natural regulation of animal numbers*. Clarendon.
- Lambert, C. M., Wielgus, R.B., Robinson, H.R., Cruickshank, H.S., Clarke, R., Almack, J., 2006. Cougar population dynamics and viability in the Pacific Northwest. *Journal of Wildlife Management* 70, 246-254.

- Laundre, J., Clark, T.W., 2003. Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation* 6, 159-170.
- Logan, K.A., Sweanor, L.L., 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press.
- Martorello, D.A., Beausoleil, R.A., 2003. Characteristics of cougar populations with and without the use of dogs. In Beacker, S.A., Bjornlie, D.D., Lindzey, F.G. and Moody, D.S. (Eds.), *Proceedings of the Seventh Mountain Lion Workshop*, May 15-17, 2003. Wyoming Game and Fish Department, Lander, Wyoming, USA. pp. 129-135.
- Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology* 21, 36-47.
- Murphy, K.M., Ross, R.I., Hornocker, M.G. 1999. The ecology of anthropogenic influences on cougars. In: Clark, T.W., Curlee, A.P., Minta, S.C., Kareiva, P.M. (Eds.), *Carnivores in Ecosystems: The Yellowstone Experience*. Yale University Press. pp.77-101.
- Packer, C., Pusey, A.E., 1983. Adaptations of female lions to infanticide by incoming males. *The American Naturalist* 121, 716-728.
- Peek, J.M., 1986. A review of wildlife management. Prentice-Hall.
- Pierce, B.M., Bleich, V.C., Bowyer, R.T., 2000b. Social organizations of mountain lions: Does a land-tenure system regulate population size? *Ecology* 81, 1533-1543.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* 18, 1028-1037.

- Ross, P.I., Jalkotzy, M.G., 1992. Characteristics of a hunted population of cougars in Southwestern Alberta. *Journal of Wildlife Management* 56, 417-426.
- Sargeant, G.A., Ruff, R.L. 2001. Demographic response of black bears at Cold Lake, Alberta, to the removal of adult males. *Ursus* 12:59-68.
- Seidensticker, J.C., Hornocker, M.G., Wiles, W.V., Messick, J.P., 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* 35, 1-60.
- Sinclair, A.R.E. 1977. *The African buffalo*. University of Chicago Press.
- Smith, J.L.D., McDougal C., 1991. The contribution of variance in lifetime reproduction to effective population size in tigers. *Conservation Biology* 5, 484-490.
- Spreadbury, B.R., Musil, K., Musil, J., Kaisner, C. Kovak, J., 1996. Cougar population characteristics in southeastern British Columbia. *Journal of Wildlife Management* 64, 962-969.
- Staines, B.W., 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). *Journal of Zoology* 184, 403-419.
- Stoner, D.C., Wolfe, M.L., Choate, D.M., 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. *Journal of Wildlife Management* 70, 1588-1600.
- Strickland, M.D, Harju, H.J., Mccaggery, K.R., Miller, H.W., Smith, L.M., Stoll, R.J., 1994. Harvest management. In: Theodore, A. Bookhout (Ed.), *Research and management techniques for wildlife and habitats*. The Wildlife Society, Inc., Allen Press, pp: 445-473.
- Sweanor, L.L., Logan, K.A., Hornocker, M.G., 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. In: Festa-Bianchet, M., Apollonio, M. (Eds.), *Animal Behavior and Wildlife Conservation*. Island Press.
- Waters, L.A. Lens, L., 1995. Effects of food availability and density on red squirrel (*Sciurus Vulgaris*) reproduction. *Ecology* 76, 2460-2469.
- White, G.C., Bartmenn, R.M., 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *Journal of Wildlife Management* 62, 214-225.
- Whitman, K.L., Starfield, A.M., Quadling, H., Packer, C., 2007. Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology* 21, 591-601.
- Wielgus, R.B., Bunnell, F.L., 1994. Dynamics of a small, hunted brown bear (*Ursus arctos*) population in southwestern Alberta, Canada. *Biological Conservation* 67:161-166.
- Wielgus, R.B., Bunnell, F.L., 1985. Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59, 552-560.
- Winterstein, S.R., Pollock, K.H., Bunk, C.M., 2001. Analysis of survival data from radiotelemetry studies. In: Millspaugh, J.J. and Marzluff, J.M. (Eds.), *Radio Tracking and Animal Populations*. Academic Press. pp. 51-380.
- Wolff, J.O., 1997. Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology* 66, 1-13.
- Zar, J.H., 1999. *Biostatistical analysis*. Fourth edition. Prentice-Hall.
- Zimmerman, F., Breitenmoser-Wursten, C., Breitenmoser, U., 2005. Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. *Journal of Zoology* 267, 381-395.

Table 2.1. Mortality rates (mean  $\pm$  SD) and sample sizes (number of dead animals in parentheses) of radio-collared cougars in northeast and central Washington, 2002 - 2007.

	Northeast WA				Central WA			
	n	Hunting	Depredation	Natural	n	Hunting	Vehicle	Natural
<b>FEMALE</b>								
<b>Kitten (0-12 mos.)</b>	10		0.14 $\pm$ 0.13 (1)	0.54 $\pm$ 0.18 (4)	6			0.28 $\pm$ 0.24 (1)
<b>Juv. (13-24 mos.)</b>	6				5	0.24 $\pm$ 0.21 (1)		
<b>Adult (24+ mos.)</b>	19	0.22 $\pm$ 0.07 (7)		0.12 $\pm$ 0.06 (4)	12	0.04 $\pm$ 0.04 (1)		0.09 $\pm$ 0.06 (2)
<b>Total</b>	35	0.16 $\pm$ 0.05 (7)	0.02 $\pm$ 0.02 (1)	0.18 $\pm$ 0.06 (8)	23	0.07 $\pm$ 0.05 (2)		0.10 $\pm$ 0.05 (3)
<b>MALE</b>								
<b>Kitten (0-12 mos.)</b>	13			0.69 $\pm$ 0.14 (6)	13			0.47 $\pm$ 0.17 (4)
<b>Juv. (13-24 mos.)</b>	12	0.46 $\pm$ 0.17 (4)			8	0.25 $\pm$ 0.22 (1)	0.25 $\pm$ 0.22 (1)	
<b>Adult (24+ mos.)</b>	12	0.46 $\pm$ 0.12 (8)	0.06 $\pm$ 0.24 (1)		12	0.20 $\pm$ 0.09 (4)	0.10 $\pm$ 0.07 (2)	0.05 $\pm$ 0.05 (1)
<b>Total</b>	37	0.35 $\pm$ 0.08 (12)	0.03 $\pm$ 0.03 (1)	0.17 $\pm$ 0.06 (6)	33	0.16 $\pm$ 0.06 (5)	0.09 $\pm$ 0.05 (3)	0.16 $\pm$ 0.06 (5)
<b>Population Totals</b>	72	0.24 $\pm$ 0.05 (19)	0.03 $\pm$ 0.02 (2)	0.18 $\pm$ 0.04 (14)	56	0.11 $\pm$ 0.04 (7)	0.05 $\pm$ 0.03 (3)	0.13 $\pm$ 0.04 (8)

Table 2.2. Radio-days, sample size (number of mortalities and total number of monitored animals in parentheses), and survival rates (mean  $\pm$  SD) by sex and age class for radio-collared cougars in northeast and central Washington, 2002-2007.

	Northeast WA			Central WA		
	Radio days	N	Survival rate	Radio days	n	Survival rate
<b>Female</b>			<b>Northeast</b>			
Kitten (0-12 mos.)	1611	5 (10)	0.32 $\pm$ 0.16	1094	1 (6)	0.7162 $\pm$ 0.24
Juvenile (13-24 mos.)	1871	0 (6)	1.00 $\pm$ 0.00	1310	1 (5)	0.7567 $\pm$ 0.21
Adult (24+ mos.)	9645	11 (19)	0.66 $\pm$ 0.08	7601	3 (12)	0.8658 $\pm$ 0.07
Total	13126	16 (35)	0.64 $\pm$ 0.07	10005	5 (23)	0.8332 $\pm$ 0.07
<b>Male</b>						
Kitten (0-12 mos.)	1885	6 (13)	0.31 $\pm$ 0.15	2295	4 (13)	0.5290 $\pm$ 0.17
Juvenile (13-24 mos.)	2392	4 (12)	0.54 $\pm$ 0.52	1084	2 (8)	0.5095 $\pm$ 0.24
Adult (24+ mos.)	4470	9 (12)	0.48 $\pm$ 0.12	5851	7 (12)	0.6461 $\pm$ 0.11
Total	8746	19 (37)	0.45 $\pm$ 0.08	9230	13 (33)	0.5978 $\pm$ 0.08
<b>Population Totals</b>	21872	35 (72)	0.56 $\pm$ 0.05	19235	18 (56)	0.71 $\pm$ 0.06

Table 2.3. Densities and ages (mean  $\pm$  SD) for monitored cougars in northeast and central Washington, 2002 - 2007.

	Sex	Northeast WA		Central WA	
		Density (cougars/100km <sup>2</sup> )	Age (months)	Density (cougars/100km <sup>2</sup> )	Age (months)
Adults (> 24 months)	Female	1.35 $\pm$ 0.12	51 $\pm$ 7	1.07 $\pm$ 0.38	68 $\pm$ 13
	Male	0.23 $\pm$ 0.10	42 $\pm$ 5	0.80 $\pm$ 0.05	59 $\pm$ 6
	Total	1.58 $\pm$ 0.17	48 $\pm$ 5	1.87 $\pm$ 0.42	61 $\pm$ 4
All Ages	Female	2.83 $\pm$ 0.76	33 $\pm$ 7	2.32 $\pm$ 0.44	40 $\pm$ 6
	Male	0.63 $\pm$ 0.12	24 $\pm$ 5	1.30 $\pm$ 0.15	40 $\pm$ 5
	Total	3.46 $\pm$ 0.69	27 $\pm$ 4	3.62 $\pm$ 0.58	38 $\pm$ 4

Table 2.4. Effects of study area (Northeast and Central Washington) and time (2001 – 2007) on density (cougars/100km<sup>2</sup>) estimates of cougars using a general linear model.

Parameter	Estimate	SE	t-value	P-value
Total Cougars				
Intercept	4.05	0.38	10.71	< 0.01
Area 1	0.65	0.54	1.21	0.26
Area 2	0.00	*	*	*
Time	-0.15	0.10	-1.53	0.17
Time*Area 1	-0.27	0.14	-1.94	0.09
Time*Area 2	0.00	*	*	*
Male Cougars				
Intercept	1.41	0.14	10.17	< 0.01
Area 1	-0.78	0.20	-3.97	< 0.01
Area 2	0.00	*	*	*
Time	-0.04	0.04	-1.04	0.33
Time*Area 1	0.02	0.05	0.47	0.65
Time*Area 2	0.00	*	*	*
Female Cougars				
Intercept	2.64	0.33	7.92	< 0.01
Area 1	1.43	0.47	3.02	0.02
Area 2	0.00	*	*	*
Time	-0.11	0.09	-1.30	0.23
Time*Area 1	-0.29	0.12	-2.38	0.04
Time*Area 2	0.00	*	*	*

Area 1 = Northeast

Area 2 = Central

## **CHAPTER THREE**

### **A COMPARISON OF METHODS FOR ASSESSING CARNIVORE DENSITY FROM RADIO COLLAR DATA**

## **ABSTRACT**

Density estimates of carnivore populations may not be comparable because of differences in study area size and scale, and surrounding landscape features that restrict animal movements. Radio telemetry and Global Positioning System (GPS) can improve estimates by defining study area boundaries from animal locations and accounting for animal movements inside and outside of the boundary. As part of a 6-year study investigating effects of hunting on cougar (*Felis concolor*) demography, I compared density estimates of two independent, radio-collared cougar populations in Washington. I calculated densities using three different methods and compared the results between study areas. Method 1 estimated density by the number of animals within a predefined study area; Method 2 used the number of animals located within the 95% composite range of females; and Method 3 used the proportional number of GPS locations from each animal that fell within the composite range of females. Methods 1 and 2 overestimated total cougar density in one area and overestimated densities of males in both areas. My findings suggest that density calculations counting proportional numbers of animal locations within the study area boundaries for the 95% composite range of females may provide more accurate estimates that can be compared among populations.

## INTRODUCTION

Cougar (*Felis concolor*) managers depend on accurate and comparable density estimates to interpret population status and distribution. However, many estimates are not accurate and comparable because study areas vary by size and scale (Blackburn and Gaston 1997, Smallwood and Schonewald 1988, Smallwood 1997). Additionally, density estimates that do not account for the proportion of time animals spend inside the study area can result in overestimates (McLellan 1989). For example, an animal that spent only 5% of its time in a study area would count as one whole animal - the same as an animal that spent 100% of its time in the area. Radiotelemetry and Global Positioning System (GPS) collars can improve effectiveness of density estimates by defining study area boundaries from animal location data and accounting for the time animals spend within the boundary.

I compared density estimates of two independent populations of GPS-collared cougars in Washington from 2002 - 2007. I calculated densities using three different methods to assess which would provide the most reliable comparisons. My first method estimated densities of cougars from the number of animals located within a subjective predefined study area, often defined by physiographic and human imposed boundaries such as administrative boundaries, highways, etc. Carnivore studies that attempt to count all animals commonly use this method to detect changes in density (Robinson et al. 2008, Stoner et al. 2006, Logan and Sweanor 2001, Ross and Jalkotzy 1992, Servheen 1983). To derive density estimates that may be more ecologically based, I used the 95% composite range for females as the study area boundary (Wielgus et al. 1994, Wielgus and Bunnell 2000, Hellgren et al. 2005, Lambert et al. 2006). Finally, I propose a third

method that accounted for animal movements beyond the study area boundary and used the proportional number of GPS locations for each animal that fell within the composite female range and not the number of animals inside the study area boundary.

## **STUDY AREAS**

I monitored cougar populations in two study areas > 250 km apart and managed under different hunting strategies (Fig 3.1). Heavy hunting with the aid of hounds (hunting mortality rate = 0.24, see Chapter 2) was permitted in the Northeast Washington area and light hunting without the use of hounds (hunting mortality rate = 0.11, see Chapter 2) was permitted in the Central Washington study area.

### Northeast Area

The 735 km<sup>2</sup> study area lies north of the town of Kettle Falls, and includes a patchwork of federal, state, and privately owned lands. The study area is bounded on the southeast and southwest by the Columbia and Kettle Rivers. The Canadian-United States border forms the northern boundary. The area is part of a glacially subdued mountainous region (400-2,130 m elevation) known as the Okanogan Highlands, and occupies the transition between the East-slope Cascades and Northern Rocky Mountain physiographic province (Bailey et al., 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the 46 cm annual precipitation falls as snow with an average of 136 cm falling from mid-November to mid-April annually. Mean annual temperatures ranges from -6°C in January to 21°C in July.

## Central Area

The study area is located along the east slope foothills of the North Cascades Mountains near the town of Cle Elum. The area covers 594 km<sup>2</sup> and includes a portion of the upper Yakima River watershed. The Cascade Mountains form the western boundary, the Enchantment Wilderness forms the north and unforested agricultural lands of the Kittitas Valley form the south and east. Sagebrush steppe foothills (below 550 m elevation) transition upwards to ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) covered slopes. Sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) dominate ridges at elevations > 1550 m. Precipitation averages 56.4 cm/yr, with 160 cm of snowfall during winter). Mean annual temperature ranges from -7°C in January to 27°C in July.

## **METHODS**

I attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of each study area during winter when tracks are detected in snow. I used hounds to track and tree cougars in winter (Hornocker 1970). I immobilized cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 ml/10 kg of body mass, or with Telazol at a dosage of 6 mg/kg, using a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). I recorded sex and determined age from gum regression measurements (Laundre et al. 2000) and assigned age classes to kittens (0-12 months), juveniles (13-24 months), and adults (25+ months).

I fitted animals with a mortality-sensing GPS collar (Lotek Wireless Inc, Newmarket, Ontario and Televilt, Lindesberg, Sweden) or VHF collar (Advanced Telemetry Systems, Isanti MN). Beginning in January 2005 I investigated den sites of collared females, and captured kittens by hand. I collared kittens that were >6-weeks old with expandable VHF (Telonics Inc, Mesa, AZ; T. Ruth personal communication 2004) radio collars to accommodate growth (Telonics Inc, Mesa, AZ; T. Ruth design 2004). I handled all animals in accordance with Washington State University Animal Care (IACUC Permit #3133) and Animal Welfare Assurance Committee (AWAC Permit #A3485-01). GPS collars were programmed to collect locations at 4 hour intervals (6 times/day). The data were retrieved using a remote data retrieval radio receiver. I recorded location coordinates of VHF-collared animals at one-week intervals from ground or aerial telemetry.

Despite attempts to systematically search and mark animals, I was not able to mark the entire population. Therefore, to establish a minimum population estimate for each study area I included demographic data from collared and uncollared cougars that were harvested by hunters, killed during depredation hunts, and killed by vehicle collisions (Stoner et al. 2006, Robinson et al. 2008). I back-calculated the lifespan of each marked and unmarked cougar to the beginning of the study, its birth date, or immigration date as described by Logan and Sweanor (2001:66), Stoner et al. (2006), and Robinson et al. (2008). I estimated cougar densities (cougars/100 km<sup>2</sup>) from the cougar count data using 3 methods.

Method 1 estimated mean annual densities of cougars/100 km<sup>2</sup> from the number of animals captured and mortalities of unmarked animals within the predefined study area

(game management unit for Northeast, watershed for Central). This method is commonly used in large carnivore studies that attempt to count all animals (Robinson et al. 2008, Stoner et al. 2006, Logan and Sweanor 2001, Ross and Jalkotzy 1992, Servheen 1983).

Method 2 derived a second density estimate as cougars/100 km<sup>2</sup> within the mean annual 95% composite fixed-kernel range of radio-marked females (Lambert et al. 2006). I used only female ranges because males typically maintain territories that are much larger than that for females (Logan and Sweanor 2001), making it impractical to thoroughly survey and mark all animals within the composite male home range. The female composite home range provides a study area boundary that is ecologically meaningful (Wielgus et al. 1994, Wielgus and Bunnell 2000, Hellgren et al. 2005, Lambert et al. 2006).

Method 3 calculated density using the proportional number of locations for each animal (McLellen 1989) that fell within the mean annual composite 95% fixed-kernel range for female cougars. I calculated the composite range for each year using ArcGIS 9.2 (ESRI, Redlands, CA). I plotted all cougar GPS locations for the corresponding year and calculated the proportion of male and female points within this composite range. This permitted me to account for the fact that the study areas were not closed.

I used factorial analysis of variance (ANOVA) models to test for effects of the 3 methods and 2 study areas on cougar density estimates. Factors were method, area, and year. I tested differences in the least square means among treatments with post hoc Tukey comparisons. Analyses were performed using SAS version 9.1.3 (SAS Institute,

Cary, North Carolina, USA). I used linear regression to examine changes in density among years (Zar 1999).

## RESULTS

I captured and marked 103 cougars in the 2 study areas (57 in Northeast, 46 in Central) over a 71-month period from 2002 - 2007. Hunters killed 50 unmarked cougars (9 females, 13 males in Northeast; 14 females, 13 males, 1 unknown sex in Central), and 1 unmarked female was killed by a vehicle collision in Central. I observed 26 unmarked kittens (6 females, 2 males, and 9 unknown sex in Northeast; 3 females, 4 males, and 2 unknown sex in Central) traveling with collared females.

The mean annual 95% composite female range for Northeast covered 772 km<sup>2</sup> (95% CI = 316 – 1228) and 655 km<sup>2</sup> (95% CI = 425 – 885) for Central. The mean annual proportion of male GPS points within the female composite home range was 0.32 (95% CI = 0.16 - 0.47) in Northeast and 0.43 (CI = 0.12 – 0.74) in Central.

Cougar density estimates for all age classes in the relatively closed Northeast area using the 3 methods ranged from 2.87 – 3.25 cougars/100 km<sup>2</sup>. For the relatively open Central area density estimates ranged from 3.53 – 5.78 cougars/100 km<sup>2</sup> (Table 3.1). The analysis of variance revealed no interaction for method by year for all categories ( $p > 0.05$ ). There was an interaction between method and study area for total cougar density ( $F_{2,10} = 6.45$ ,  $p = 0.02$ ) and male density ( $F_{2,10} = 35.34$ ,  $p < 0.01$ ), but not for female density ( $F_{2,10} = 0.68$ ,  $p = 0.53$ ). Total cougar densities in Central were significantly higher than in Northeast using Methods 1 and 2, but not with Method 3 (Method 1:  $t = 11.32$ ,  $p < 0.01$ ; Method 2:  $t = 10.24$ ,  $p < 0.01$ ; Method 3:  $t = 1.17$ ,  $p = 0.27$ ). Densities

of males in Central (1.28 – 3.12 cougars/100km<sup>2</sup>) were higher than in Northeast (0.59 – 1.95 cougars/100km<sup>2</sup>) using all methods ( $p < 0.05$ , Table 3.2). Female densities in Central (2.25 – 2.67 cougars/100km<sup>2</sup>) were not significantly different ( $p > 0.05$ , Table 3.2) from the Northeast (2.67 – 2.95 cougars/100km<sup>2</sup>).

All 3 methods produced similar ( $p > 0.05$ ) estimates for total cougar density in the Northeast area but Method 3 produced a lower ( $p < 0.01$ ) estimate of cougar density than Methods 1 and 2 in the open Central area (Table 3.2). Method 3 also produced lower estimates for males in both areas ( $p < 0.01$ ). All three methods detected a decline in female density in Northeast over time (Method 1:  $F = 7.96$ ,  $p = 0.05$ ,  $R^2 = 0.67$ , for all regressions, MS regression  $df = 1$ ; MS residual  $df = 4$ ; Method 2:  $F = 7.36$ ,  $p = 0.05$ ,  $R^2 = 0.65$ ; Method 3:  $F = 7.36$ ,  $p = 0.05$ ,  $R^2 = 0.67$ ). Only Method 3 detected a decline in total cougar density for Northeast (Method 1:  $F = 2.86$ ,  $p = 0.17$ ,  $R^2 = 0.42$ ; Method 2:  $F = 2.86$ ,  $p = 0.17$ ,  $R^2 = 0.42$ ; Method 3:  $F = 68.09$ ,  $p = 0.001$ ,  $R^2 = 0.95$ ). Male densities in Northeast did not change using any method and I detected no changes in any classes for Central.

## **DISCUSSION**

Density of cougars in 2 Washington populations using number of cougars within a predefined study area (Method 1) and number of cougars within composite range of females (Method 2) produced higher estimates for males in both areas and of total cougars for Central. Calculations using Method 1 and Method 2 provided similar estimates, probably because the areas were similar in size. The size of the predefined study area and 95% composite home range in Northeast differed by only 35 km<sup>2</sup> and the

Central areas differed by 61 km<sup>2</sup>. If the differences in size had been larger, I probably would have detected greater variation between Methods 1 and 2. Method 3 (proportion of time spent in 95% composite range of females) significantly reduced density estimates for several sex and age classes, including adult male and total male densities in both areas, and total cougar densities in Central.

Computing densities from the proportion of animal locations within the study area (Method 3) can account for differences in landscape boundaries and animal geospatial distribution. Total cougar densities in Central appeared higher than in Northeast using Methods 1 and 2, but were not different using Method 3. Methods 1 and 2 produced estimates for total cougar density that were 39% higher than Method 3 (5.78 vs. 3.53 cougars/100 km<sup>2</sup>). Estimates of adult males were 72% higher (2.83 vs. 0.80 cougars/100 km<sup>2</sup>) using Methods 1 and 2. This discrepancy is likely caused by the open nature of the Central area. In contrast, density estimates differed for Northeast by only 11%, probably because of the more naturally confining geography. This study area was bounded by 2 major river systems that restrained cougar movements and home range size.

I expected density estimates using Method 3 to be lower because animals often travel beyond study area boundaries, so the proportion of locations within the study area boundary can be < 1.0 (Figs 3.2 and 3.3). This method affected estimates of males, in particular, which spent less time in the study area due to their more extensive movements. Thirty-two percent of male locations in Northeast WA and 43% in Central WA were within the study area boundary, resulting in a significant drop in densities. These findings reveal that failure to account for the actual amount of time animals spend inside

the study area boundary can result in overestimates of density. For example, 1 male spending time in 2 adjacent study areas would count as 2 males using Methods 1 and 2.

The Central study area was surrounded on all sides by forested habitat that did not present a barrier to animal movements, with home ranges of several animals straddling the study area boundary. This contrasts with the Northeast that was bounded on two sides by large rivers. Although males did disperse across these rivers, home ranges did not transect them. Such natural barriers can influence movements and density estimates for carnivores (Smallwood and Schonewald 1988, Smallwood 1997). Low quality habitat or natural barriers may restrict animal movements within study areas. Alternatively, study areas bounded by confining landscape features do not restrict movements. These differences can lead to erroneous comparisons if density estimates are based on numbers of animals vs. proportions of their locations.

## **MANAGEMENT IMPLICATIONS**

Carnivore managers rely on density estimates to set harvest quotas and other management prescriptions. However, many studies report crude density estimates (number of animals/size of study area) that overestimate density and are not directly comparable to other areas. I encourage researchers investigating carnivore density to use Method 3 (the proportion of animal locations within the composite range for females), for estimating density, population size, and determining harvest quotas.

## LITERATURE CITED

- Bailey, R. G., P.E. Avers, T. King, and W.H. McNab, editors. 1994. Ecoregions and subregions of the United States (map). Washington, DC: USDA Forest Service. 1:7,500,000.
- Blackburn, T.M. and K.J. Gaston. 1997. Who is rare? Artifacts and complexities of rarity determination. *in* K.J. Gaston W.E. Kunin, editors. The biology of rarity. Chapman and Hall, London, England.
- Hellgren, E.C., D.P. Oronato, and J.R. Skiles. 2005. Dynamics of a black bear population within a desert metapopulation. *Biological Conservation* 122:131-140.
- Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 21. The Wildlife Society, Lawrence, Kansas, USA.
- Lambert, C. M., R. B. Wielgus, H. S. Robinson, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. *Journal of Wildlife Management* 70:246-254.
- Laundre, J. and T.W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation* 6:159-170.
- Logan, K.A. and L. L. Swenor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C., USA.
- McLellan, B.N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. *Canadian Journal of Zoology* 67:1856-1860.

- 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.
- Servheen, C. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *Journal of Wildlife Management* 47:1026-1035.
- Smallwood, K.S. 1997. Interpreting puma (*Puma concolor*) population estimates for theory and management. *Environmental Conservation* 24:283-289.
- Smallwood, K.S. and C. Schonewald. 1998. Study design and interpretation of mammalian carnivore density estimates. *Oecologia* 1998:474-491.
- 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., 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.
- Wielgus, R.B., F.L. Bunnell, W.L. Wakkinen, and P.E. Zager. 1994. Population dynamics of Selkirk mountain grizzly bears. *Journal of Wildlife Management* 58:266-272.
- Wielgus, R.B., and F.L. Bunnell. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation* 93:145-154.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River,  
New Jersey, USA.

Figure 3.1. Central Washington study area and the Northeast Washington study area.

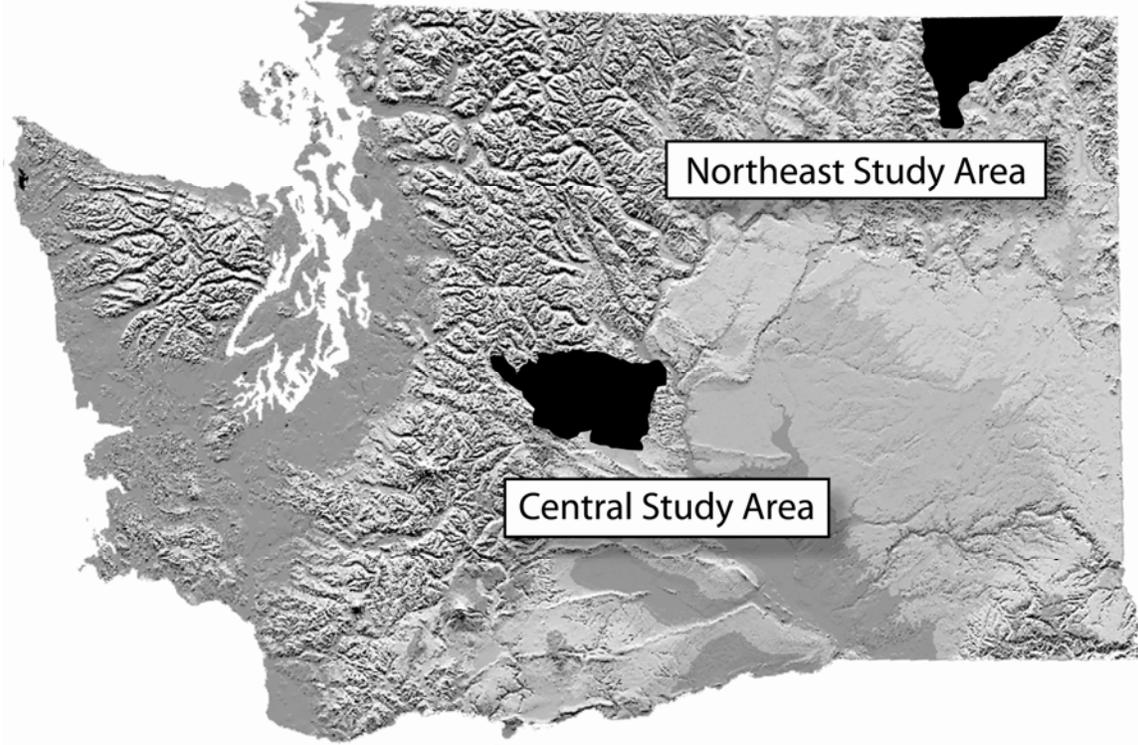


Figure 3.2. The Northeast Washington study area showing the predefined study area boundary (solid double line), 95% composite range for female cougars (dashed line), and male GPS points (circles) used to calculate cougar densities. Landscape features, such as the Columbia and Kettle Rivers confine cougar movements.

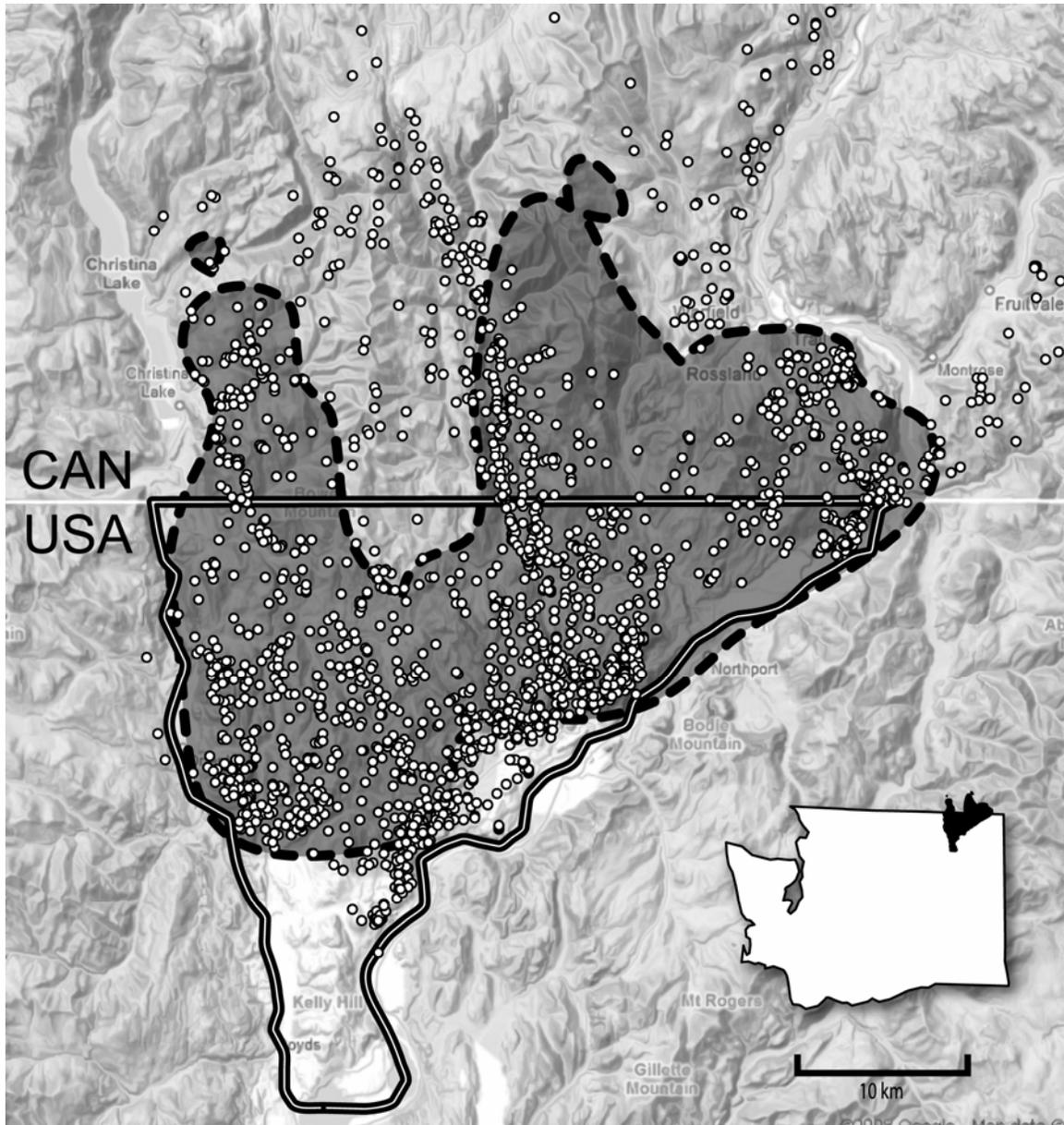


Fig 3.3. The Central Washington study area showing the predefined study area boundary (solid double line), 95% composite range for female cougars (dashed line), and male GPS points (circles) used to calculate cougar densities. A lack of confining landscape features allow cougar movements to cross study area boundaries.

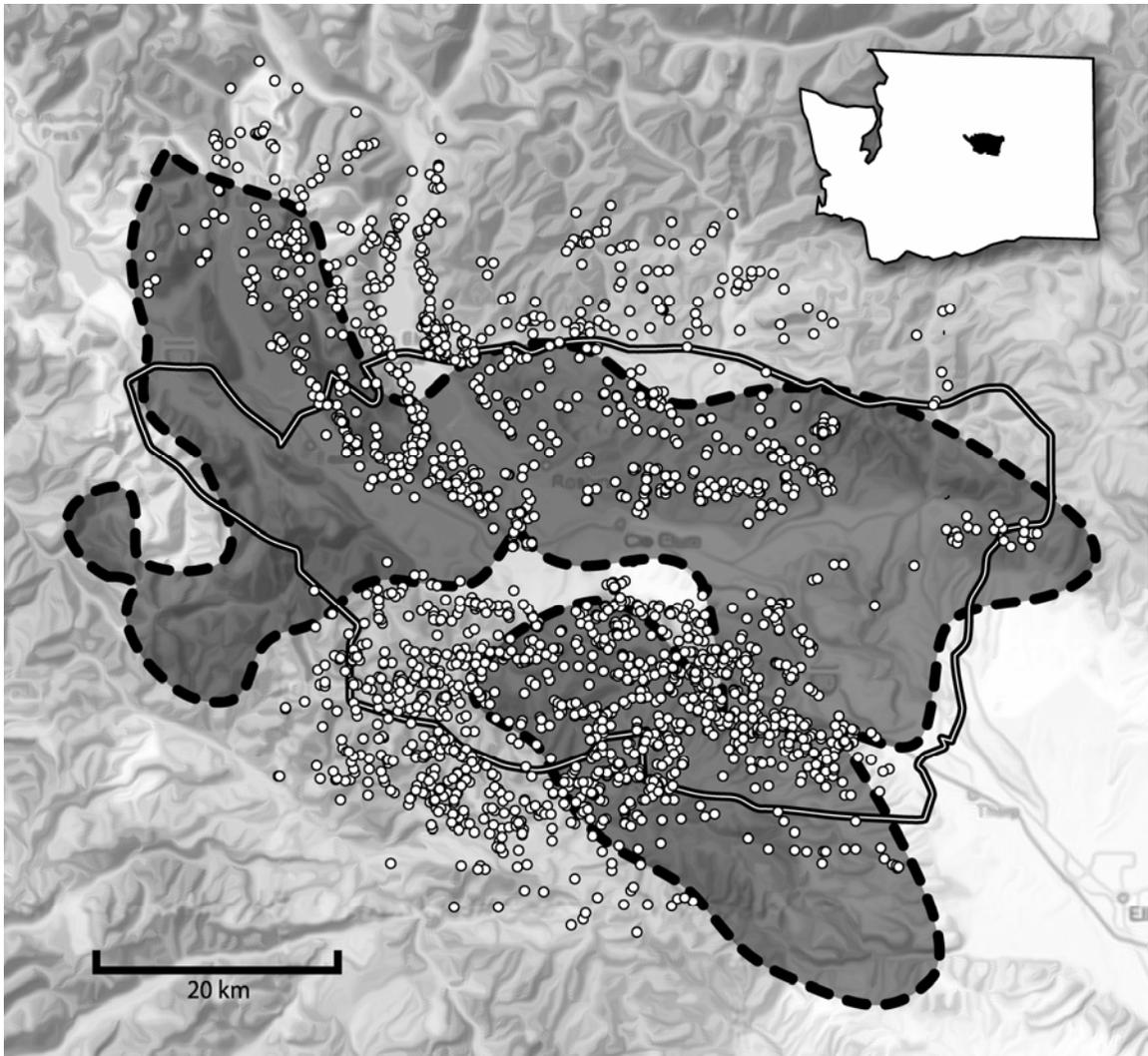


Table 3.1. Mean densities of cougars (cougars/100km<sup>2</sup>) in 2 study areas (CE = Central, NE = Northeast) in Washington from 2002-2007, using 3 methods: Method 1 estimated densities using the number of animals within a predefined study area; Method 2 estimated densities using the number of animals within the 95% composite range of females; Method 3 estimated densities using the proportion of GPS locations that fell inside the composite female range.

Method	Area	Total Cougars		Males		Females	
		Density	SE	Density	SE	Density	SE
1	CE	5.78	0.39	3.12	0.18	2.67	0.23
2	CE	5.37	0.31	3.00	0.13	2.37	0.18
3	CE	3.54	0.23	1.28	0.06	2.25	0.17
1	NE	3.02	0.30	1.95	0.21	2.95	0.36
2	NE	2.87	0.28	1.86	0.20	2.81	0.34
3	NE	3.25	0.33	0.59	0.06	2.67	0.32

Table 3.2. Comparisons of cougar densities (cougars/100km<sup>2</sup>) in 2 study areas (CE = Central, NE = Northeast) in Washington from 2002-2007, using 3 methods: Method 1 estimated densities using the number of animals within a predefined study area; Method 2 estimated densities using the number of animals within the 95% composite range of females; Method 3 estimated densities using the proportion of GPS locations that fell inside the composite female range.

AREA	METHOD	Total Cougars		Males		Females	
		t value*	P	t value*	P	t value	P
CE	1 vs. 2	1.80	0.10	1.08	0.30	2.93	0.01
CE	1 vs. 3	9.82	< 0.01	17.52	< 0.01	4.08	< 0.01
CE	2 vs. 3	8.02	< 0.01	16.44	< 0.01	1.14	0.28
NE	1 vs. 2	0.64	0.54	0.89	0.39	1.40	0.19
NE	1 vs. 3	-1.01	0.34	13.03	< 0.01	2.77	0.02
NE	2 vs. 3	-1.65	0.13	12.14	< 0.01	1.37	0.20
NE vs. CE	1	-11.32	< 0.01	-6.63	< 0.01	0.78	0.46
NE vs. CE	2	-10.24	< 0.01	-6.51	< 0.01	1.21	0.25
NE vs. CE	3	-1.17	0.27	-3.96	< 0.01	1.14	0.28

\* DF for all comparisons = 10