

DYNAMICS AND VIABILITY OF A COUGAR POPULATION  
IN THE PACIFIC NORTHWEST

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of  
CATHERINE MARIE SARAH LAMBERT find it satisfactory and recommend that  
it be accepted.

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Chair

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DYNAMICS AND VIABILITY OF A COUGAR POPULATION  
IN THE PACIFIC NORTHWEST

Abstract

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Cougar (*Puma concolor*) populations are believed to be at high density and increasing throughout western North America, especially in the Pacific Northwest, as evidenced by increasing cougars/humans encounters. Harvest rates have increased as a result. To test this hypothesis, I determined the density, fecundity, survival, and growth rate of a cougar population in northeastern Washington, northwestern Idaho, and southern British Columbia. From 1998 to 2003, 52 cougars were captured, radio-collared, and monitored. I recorded fecundity through den site investigation and snow tracking, and mortality by weekly telemetry. Survival rates were estimated for kittens (0-1 yr), yearlings (1-2 yr), and adult (2-12 yr) males and females. Average overall density was 1.09 cougars/100km<sup>2</sup> or 0.46 adults/100km<sup>2</sup>. I estimated the litter size at 2.53 kittens, the birth interval at 18 months, the proportion

of reproductively successful females at 0.75, and the age of first reproduction at 30 months, for a maternity rate of 0.63 male or female kitten/year/adult female. Average survival rate for all radio-collared cougars was 0.59, 0.77 for adult females, 0.44 for adult males, 0.37 for yearlings, and 0.57 for kittens. Hunting accounted for 92% of the mortalities of radio-collared cougars. Age- and sex-specific survival and fecundity were entered into a stochastic two-sex matrix model. I used computer simulations to determine the stochastic growth rate of the population and to assess its viability over 25 years. The annual stochastic growth rate of this population was  $\lambda = 0.80$  (95%CI = 0.11). Starting with a total initial abundance of 357, the median times to fall below a demographic collapse ( $N = 30$  adults) and extirpation ( $N = 0$ ) were 8.5 and 25.9 years. My findings suggest that, contrary to popular belief, cougars in the Pacific Northwest are currently at low to moderate densities and are declining. Alternative hypotheses may account for the increased conflicts between cougars and humans in this area.

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## **Dedication**

I dedicate this thesis to the Cougars themselves

–fascinating, powerful, vulnerable animals–

May they be inhabit our forests and mountains for the centuries to come...

*Go confidently in the direction of your dreams. Live the life you have imagined.*

*-Henry David Thoreau (1817 - 1862)*

## INTRODUCTION

Cougar (*Puma concolor*) populations are believed to be increasing throughout western North America (Riley and Malecki 2001), as evidenced by the increased frequency of reported encounters with humans (Beier 1991, Chester 2003) and number of cougar harvested (Dawn et al. 2003). This is especially true in Washington state (WA), where there is a current controversy about harvest regulations (Martorello 2003). Although bounties for predators were abolished in 1960, the number of cougars hunted in the state during the past century has increased steadily (Spencer et al. 2001). In 1996, hunting with hounds became illegal after voter initiative 655 was passed, but the hunting season's length and bag limit were both increased to compensate. The years following initiative 655 were marked by a constant increase in the number of complaints related to interactions between humans and cougars –annual registered complaints rose from 247 in 1995 (the year before the ban) to 495 in 1996, and 927 in 1998 (Washington Department of Fish and Wildlife 1999). Since then, complaints have averaged about one thousand a year. Because of increased complaints, the Engrossed Substitute Senate Bill (ESSB) 5001 was passed in 2001, allowing the use of hounds for safety removals. The 2001 Washington game status report (Martorello 2001) suggested that cougars were stable to increasing statewide and were moderately exploited, so hunting regulations have

continued to become more permissive. To further satisfy local concerns, emergency cougar hunts were adopted in March 2003 in Stevens, Ferry and Okanogan Counties, in northeastern WA. Recent reports from neighboring Idaho (ID) (Nadeau 2003) and British Columbia (BC) (Austin 2003) showed that hunting effort has also been constantly increasing from 1998 to 2002, with harvest rates as much as 700% higher than 20 years ago.

Many hypotheses were proposed to account for the increase number of cougar complaints in WA. The most popular belief is that this indicates a very high cougar density and increasing cougar population. Alternatively, more frequent encounters and complaints may be caused by encroachment of expanding suburbs into cougar habitat (Dickson and Beier 2002, Spencer et al. 2001). Hunting itself could also be indirectly responsible for the increased frequency in cougar/human conflicts. Carnivore populations under heavy hunting pressure may have a very young age structure, as seen in African lions (*Panthera leo*) (Smuts 1978) and wolves (*Canis lupus*) (Jedrezejewska et al. 1996). Removing older animals can increase the density of immigrating/settling juveniles or sub-adults from adjacent areas (Wielgus et al. 2001), which are often responsible for most of the attacks on humans and livestock (Beier 1991). Finally, low levels of stakeholder acceptance of cougars can amplify the perception that cougars are increasing (Riley and Decker

2000, Riley and Malecki 2001), and the large number of complaints could be a local backlash to initiative 655.

My primary objective was to test the hypothesis that cougars are at very high density and increasing, by determining the density and growth rate of the population in northeastern WA, northwestern ID and southern BC from 1998 to 2003. I examined the vital rates of cougars in two overlapping areas. Between 1998 and 2001, 32 individuals were radio-collared and monitored in the Selkirk Mountains in northern ID (Panhandle area), southeastern BC (Kootenay region), and northeastern WA (PendOreille county) (Katnik 2002). Seven of these 32 cougars were monitored throughout the length of the study. Twenty-one other cougars were radio-collared and monitored in the Colville National Forest in northeastern WA (Ferry and Stevens counties) between 2002 and 2003.

## STUDY AREA

The study area is located in the Northern Rocky Mountain US ecosystem province (Bailey 1995) and the Southern Interior Mountains ecoprovince of British Columbia (Demarchi 1996) (Fig.1). The minimum convex polygon of all cougar locations in this study encompassed approximately 32,800 km<sup>2</sup> (48°21'N-49°35'N, 115°57'W-119°04'W), but the composite 95% contour kernel estimate for all animals was only 5,600 km<sup>2</sup>. The area is characterized by rugged terrain with numerous ridges (1,500-2,000 m) interspersed by valleys (500 m). Average winter temperature is 0°C and the average summer temperature is 22°C. Precipitation falls mostly in the winter and averages 510 to 1,020 mm per year.

A mixed evergreen-deciduous forest dominates the landscape. In lower elevations, western red-cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) are the dominant tree species in mature forests, with black cottonwood (*Populus balsamifera trichocarpa*) the climax in moister areas. Open mixed stands of douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) are common on more xeric south-facing slopes (Ketcheson et al. 1991). In higher elevations, white spruce (*Picea glauca*) dominates the climax forest, with subalpine



fir (*Abies lasiocarpa*) composing the understory and lodgepole pine (*Pinus contorta*) common following fire (Coupe et al. 1991).

White-tailed deer (*Odocoileus virginianus*) were the most abundant ungulate, but mule deer (*Odocoileus hemionus*, see Robinson et al. 2002), elk (*Cervus elaphus*), moose (*Alces alces*) and mountain caribou (*Rangifer tanrandus caribou*, see Katnik 2002) were also present. Common predator species, beside cougars, included coyotes (*Canis latrans*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and, to a lesser extent, grizzly bears (*Ursus arctos*), lynx (*Lynx canadensis*), and wolves (*Canis lupus*).

Cougar harvest was permitted throughout the study area but regulations varied amongst jurisdictions. In WA, the hunting season lasted from 1 August to 15 March from 1998 to 2003. Hounds were prohibited in 1998, but their use was reintroduced in 2000 to meet public safety needs. In ID, the hunting season lasted from 15 September to 31 March for the 1998-99 and 1999-2000 seasons, and from 30 August to 31 March for the seasons 2000-2001 to 2002-2003. Hounds were allowed during most of the season, but starting in 1999 they were prohibited between September and December. In BC, cougar hunting in the southeastern Kootenay region lasted from 10 September to 28 February, and lasted until 31 March for the southwestern Kootenays. Hounds were allowed during the entire season.

## METHODS

### Capture and monitoring

The study area was intensively searched for cougar tracks during the snow-covered period (November to April) each year from 1998 to 2003. Hounds were released on fresh tracks and used to tree cougars (Hornocker 1970). Efforts were made to capture and collar all cougars larger than about 30kg (yearlings and adults). Treed cougars that were not too high for safe capture (those  $\leq 5$  m from the ground) were immobilized by injecting 0.4 ml/10 kg of body mass of ketamine hydrochloride (200 mg/ml) and xylazine hydrochloride (20 mg/ml), with a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). Cougars were fitted with mortality-sensing VHF radio-collars, and administered 0.2 mg/kg of body mass of yohimbine hydrochloride, a chemical antagonist of the immobilizing drugs (Seal et al. 1987). Cougars were classified either as kitten (0-1 yr), yearling (1-2 yr) or adult (2+ yrs), based on their general appearance and tooth wear (Ashman and Greer 1976). Released cougars were located about once a week by aerial or ground telemetry, from 14 December 1998 to 20 May 2003.

## **Density and abundance**

I estimated minimum mean annual density (adults/100km<sup>2</sup> and cougars/100km<sup>2</sup>) by counting all captured animals in the annual 95% adaptive kernel composite home range of the adult females (Wielgus et al. 1994), using the animal movement extension for ArcView<sup>®</sup> (ESRI, Redlands, California, U.S.A.) developed by Hooze and Eichenlaub (1997). Densities of adult females were derived from how many were monitored annually, divided by the area of their annual 95% adaptive kernel composite home range. I believe that most adult females were captured in these relatively small (1,800-5,600 km<sup>2</sup>, see Table 1) annual composite home ranges. Densities of adult males and yearlings were estimated using two different techniques. The first method counted how many animals were captured or monitored each year, divided by the adult female composite home range area. The second method, based on survival and fecundity rates, used the stable age distribution (dominant right eigenvector, Morris and Doak 2002:222) to determine the proportion of adult males and yearlings present each year, according to adult female density. These proportions were then multiplied by the number of adult females in the annual composite home range. In both cases, kitten density was assessed using the stable age distribution method. Average cougar abundance for the entire study area was obtained by extrapolating the average density estimate over the 32,800km<sup>2</sup> minimum convex polygon of all studied animals.

## **Fecundity**

The maternity rates ( $m_x$ ) were the average number of kittens of each sex ( $m_{xm}$ ,  $m_{xf}$ ) produced during 1 year by any mother of age  $x$  (Case 2000). Because cougars can reproduce all year long (birth-flow population), frequent checks of potentially reproductive females were conducted. The reproductive status at capture was determined by presence of milk in nipples, color and size of the nipples (to detect previous maternities), and sightings of kittens or yearlings. Subsequent changes in the reproductive status were detected by weekly telemetry locations. A decrease in a female's movements was investigated as a possible birth event (Beier et al. 1995, Hemker et al. 1986). I determined litter size by investigating the dens or by track counts (Banhurst and Lindzey 1989, Kerley et al. 2002, Ross and Jalkotzy 1992) for kittens from 0-3 months. I calculated annual maternity rates by dividing the average litter size by the average successful interbirth interval, and multiplying by the proportion of kitten of each sex and the proportion of reproductively successful adult females (i.e., pregnant or involved in raising a litter). The latter parameter is sometimes ignored in calculating maternity rates, but failing to consider the proportion of unsuccessfully reproducing females would bias kitten production upwards by including only successful females during short study periods (Wielgus et al. 2001). Fecundity rates ( $F_x$ ) of my post-breeding model were defined as  $F_x = m_{x+1}s_{xf}$  (Case 2000), where  $s_{xf}$  are the annual survival rates of females of age  $x$ . I

assumed  $F_x$  had the same standard deviations as  $s_{x'}$  (see below), because sample sizes were too small to estimate the standard deviations for fecundity.

## Survival

I determined the survival of kittens by comparing direct observations or track counts on snow (Kerley et al. 2002, Ross and Jalkotzy 1992) at different time intervals. Because I could not monitor kittens daily, I evaluated their survival rate as the proportion of survivors after the first year of life (365 days).

To estimate survival of radio-collared animals, I used the Mayfield method (1961) modified by Heisey and Fuller (1985), because of its high precision when vital rates are constant within time intervals (Samuel and Fuller 1996). I estimated

average annual survival rates by using the geometric mean of all years,  $\sqrt[Y]{\prod_{t=1}^Y S_t}$ ,

where  $t$  represents each year of the study,  $Y$  the total number of years, and  $S_t$  the annual survival rates. I computed the 95% confidence interval (CI) with Akçakaya's

unbiased weighed variance (2002),  $\frac{\sum_{t=1}^Y S_t(1 - S_t)}{\sum_{t=1}^Y N_t}$ , where  $N_t$  is the annual number of

cougars monitored in each class. This variance estimate minimizes sampling error and accounts for demographic stochasticity (Akçakaya 2002).

To meet the required assumption of constant mortality of the Mayfield method, I analyzed the statistical distribution of the deaths over a year (365 days) to determine the time intervals when survival probabilities were constant. This yielded two seasons: the high mortality (HM) season (13 November to 20 May) and the low mortality (LM) season (21 May to 12 November) (Fig. 2). Most of the deaths (22 of 23) during the HM season were hunting-related, whereas the only death that occurred during the LM season was caused by starvation. Intervals for each period were chosen based on the median date of the deaths for each period. I tested for differences in survival between the sex and age classes using a two-tailed *t*-test.

### **Population growth rate and short-term viability**

I constructed a post-breeding, two-sex, age-classified, stochastic matrix model to estimate annual stochastic population growth ( $\lambda$ ) and its 95%CI. I assumed that (1) environmental conditions in successive years were uncorrelated; (2) fecundity and survival rates were uncorrelated, but annual survival rates of each sex- and age-class were correlated; (3) all cougars were equally at risk within the study area (no spatial structure); (4) no catastrophes or bonanzas occurred; (5) cougars were senescent at 12 years old (Beier 1996); and (6) male density did not affect female fecundity, with the exception that a male density of 0 would cause a 0 fecundity rate. Different survival rates of adult males and females during this study

justified the use of a two-sex model (Caswell 2001). My two-sex structured model was a Leslie matrix composed of 24 classes (Fig. 3), where males and females of the same age succeeded each other from row to row and column to column (Caswell 2001), and was filled with the average vital rates for the period 1998-2003. The dominant eigenvalue of this matrix corresponds to the finite rate of increase  $\lambda_1$  of the population and the dominant right eigenvector to the stable age distribution (Caswell 2001). I assessed the relative influence of each parameter  $r$  on the population growth rate by determining and comparing their elasticity,  $E_r$ , defined as  $E_r = \frac{r}{\lambda_1} \frac{\partial \lambda_1}{\partial r}$  (Morris and Doak 2002), where  $\partial \lambda_1$  is the change in the growth rate caused by a 10% increase,  $\partial r$ , in each parameter. As part of a descriptive analysis of population growth from 1998 to 2003, I examined annual survival rates in 5 distinct matrices and calculated annual dominant eigenvalues, despite having few animals represented in each sex and age category during some years. As I didn't have sufficient data for kitten survival during some years, I used the average kitten survival rate for all annual matrices.

My model took the form  $\mathbf{n}(t) = \mathbf{L} * \mathbf{n}(t-1)$ , where  $\mathbf{n}$  is the vector of population abundance,  $t$  is the time in years, and  $\mathbf{L}$  is a Leslie matrix (Fig. 3). At time 0,  $\mathbf{n}$  was the vector of initial abundance, defined by the average density and stable age distribution extrapolated to the entire 32,800 km<sup>2</sup> study area.

Environmental stochasticity was incorporated into my model by randomly generating the  $F_x$  and  $S_x$  elements of  $\mathbf{L}$  at every time step from normal distributions with standard deviations given in a matrix  $\mathbf{V}$ . Because there was no biological reason why the variances of the average survival rates of each sex- and age-class should be different within a year, and because annual sample sizes were low for some classes, the standard deviation of annual survival rates for all radio-collared animals was used to define environmental stochasticity in  $\mathbf{V}$  (Caswell 2001).

Demographic stochasticity was included by drawing the number of survivors in each sex-age class from a binomial distribution (based on the abundance  $N_i(t)$  of each  $i^{\text{th}}$  class and on the survival rates  $s_i$  from  $\mathbf{L}$ ), and the number of kittens born each year from a Poisson distribution, using the random number generator of RAMAS 4.0 (Applied Biomathematics, Setauket, New York, USA). Age at first reproduction was set at 1.5 years (see results).

To obtain the stochastic growth rate  $\lambda$ , I projected the population 30 times over 1,000 years, or until it fell to  $N = 0$  animals. For every simulation, I computed the geometric mean of  $[N(t+1)/N(t)]$  over all pairs of adjacent years to obtain a first estimate of  $\lambda$  (Morris and Doak 2002). I selected the arithmetic mean and 95% CI of all simulations as the best estimate of the population growth rate.



I assessed population viability by examining the population trajectories of 5,000 simulations of my model projected over 25 years to determine the median time to reach the demographic collapse ( $N = 79$ ) and extirpation ( $N = 0$ ). I set demographic collapse at a total abundance of 79 cougars over the 32,800 km<sup>2</sup> area, which corresponds to an abundance of 30 adults, because populations below 30 adults are more vulnerable to Allee effects and extreme demographic stochasticity effects (Wielgus 2002). All simulations were performed with the software RAMAS 4.0.

## RESULTS

### Density and abundance

Fifty-two cougars were captured and monitored from 14 December 1998 to 20 May 2003, for a total of 19,337 cougar-radio-days and 2,737 radio-locations. Twenty were males (8 adults and 12 yearlings), and 32 were females (27 adults and 5 yearlings). Annual density estimates and trends for both methods (the annual count of monitored cougars in each class and the stable age distribution multiplied by the adult female density) were very similar (Fig. 4). Average annual density appeared to decline from a high of 1.46 cougars/100km<sup>2</sup> in 1998-99 to 0.85 cougars/100km<sup>2</sup> in 2002-03, with an average annual decline of 12±16% (mean±95% CI) (Table 1). The average density for all years was 0.46±0.24 adults/100km<sup>2</sup>, and 1.09±0.54 cougars/100km<sup>2</sup>. Total abundance in the 32,800km<sup>2</sup> study area was estimated at 357 cougars, based on 1.09 cougars/100km<sup>2</sup>. To be conservative, I used 357 as the starting point of every simulation, despite the apparent declining trend in density observed during the latter years of the study.

### Fecundity

Based on observations of 15 litters, I estimated mean litter size at 2.53±1.01. I sexed 17 kittens and found a M:F ratio of 1:1.13, not different from equality ( $z =$

0.25,  $P = 0.81$ ), so I assumed each sex represented 50% of the litter. I obtained only one successful interbirth interval (18 months), but used this value in my model because it was consistent with results from studies with larger sample sizes (17.4 months, Logan and Sweanor 2001; 17.3 months, Lopez-Gonzalez 1999; 19.7 months, Ross and Jalkotzy 1992). I estimated the age of production of the first successful litter to be 30 months, based on 29.1 months for Logan and Sweanor (2001), 30 months for Ross and Jalkotzy (1992), and 29-30 months for Spencer et al. (2001). Furthermore, I estimated that 75% of all adult females were reproductively successful (pregnant or with offspring) in any year, which could be an overestimation, considering the 41%-64% range reported by Toweill et al. (1984), Ross and Jalkotzy (1992), Robinette et al. (1961), and Toweill et al. (1988). I suspected that some births occurred without being noticed, so I remained more conservative at 75%. Based on these parameters, I estimated the maternity rate to be 0.63 kittens of each sex per year ( $\frac{2.53 \cdot 0.5 \cdot 0.75}{1.5}$ ) for females older than 2, and 0.32 for females between 1 and 2 (half the adult rate because females start to reproduce at 1.5 years old).

## Survival

Hunting accounted for 22 of the 24 deaths of radio-collared animals, and indirectly caused the death of 5 of 21 dependent kittens by death of the mother. Nine of the 52 monitored cougars were censored after losing their collars or after they moved out of the study area. Four additional individuals were excluded from all survival analyses because 1 died as a result of capture procedures and 3 others lost their radio-collar or could not be found in the study area after only one day. Overall, only 21 of the 52 radio-collared cougars lived or were monitored for longer than one year after capture. The average annual survival rate for all radio-collared cougars from 1998 to 2003 was  $0.59 \pm 0.20$ , but major variations occurred between age and sex classes, and from one year to another (Table 2). Average survival rate was higher for adult females (0.77) than for adult males (0.33) ( $t = 7.80$ ,  $df = 34$ ,  $P < 0.01$ ) or yearlings (0.34) ( $t = 10.33$ ,  $df = 43$ ,  $P < 0.01$ ). Survival did not differ between yearling males (0.37) and females (0.32) ( $t = 0.35$ ,  $df = 15$ ,  $P = 0.73$ ), so I pooled them. Yearling survival (0.34) was lower than kitten survival (0.57) ( $t = 4.92$ ,  $df = 36$ ,  $P < 0.01$ ), so I kept the two estimates distinct in my model. In total, I recorded only 2 natural mortalities for radio-collared cougars: 1 adult female was found with a broken neck and 1 adult male starved. The standard deviation of the annual rates of all radio-collared cougars was 0.17, which was used in the matrix  $V$  to incorporate environmental stochasticity in my model.

### **Population growth rate and short-term viability**

The deterministic finite rate of increase  $\lambda_1$  of the average projection matrix was 0.87. The stable age distribution was 30% adult females, 8% adult males, 25% yearlings (1:1 sex ratio), and 37% kittens (1:1 sex ratio). Overall, individuals 4 years and older represented only 22% of the population. Annual deterministic growth rates followed the pattern of adult female survival rates (Fig. 5), starting with  $\lambda_1 = 1.24$  in 1998 and then progressively declining to 1.04, 0.92, 0.59, and 0.87 in 2002-03. Elasticity analysis confirmed that adult female survival affects growth rate the most, with  $E_f = 0.69$ , whereas the elasticity value was 0 for adult males, 0.17 for yearling survival, 0.17 for kitten survival, and 0.19 for maternity rate (elasticities do not sum to 1 because both maternity and female survival rates were involved in fecundity rates).

The matrix projections yielded a stochastic population growth rate  $\lambda$  of  $0.80 \pm 0.11$  (Fig. 6). Median time to demographic collapse ( $N = 79$ ) was 8.5 years and median time to extirpation ( $N = 0$ ) was 25.9 years (Fig. 7).

## DISCUSSION

### Density

Average density estimates (0.46 adults and 1.09 cougars/100km<sup>2</sup>) were in the lower range of densities reported by other cougar researchers (from 0.44 to 13.03 cougars/100km<sup>2</sup>, Smallwood 1997). My estimates were comparable to densities observed in 2 other populations in Utah (0.37 adults/100km<sup>2</sup>, Lindzey et al. 1994; 0.96 cougars/100km<sup>2</sup>, Lopez-Gonzalez 1999), but considerably lower than those observed in 5 other populations, including Alberta (2.7 to 4.2 cougars/100km<sup>2</sup>, Ross and Jakoltzy 1992), British Columbia (3.5 to 3.7 cougars/100km<sup>2</sup>, Spreadbury et al. 1996), Idaho (2.9 adults/100km<sup>2</sup>, Hornocker 1970), and New Mexico (1.72 to 3.91 cougars/100km<sup>2</sup>, Logan and Sweanor 2001). Even the starting density, at 1.47 cougars/100km<sup>2</sup> in 1998-99, was considerably lower than most other populations, suggesting that the common perception that cougars were at very high density was incorrect.

Although intense trapping efforts were repeated each winter in an attempt to capture and radio-collar all cougars in the study area, my estimates should be considered minimum because some uncaptured individuals undoubtedly existed in the annual 95% contour kernel home range of the adult females. The progressive increase in the composite home range area may also have contributed to the observed

decline in density (Smallwood 1997). However, uncaptured animals in the 95 % composite female home range would likely be balanced by captured animals venturing outside the composite range. For example, most males spent considerable periods of time outside the adult female composite home range. Furthermore, my estimates included all animals captured every year, even cougars that were monitored for only few days. Other studies of cougar populations probably suffered the same problem of uncaptured animals and lack of population closure, so my density estimates should be directly comparable to others in the literature.

### **Demographic rates**

Litter size (2.53) was consistent with those reported elsewhere (2.4, Hemker et al. 1986; 2.4, Lindzey et al. 1994; 3, Logan and Sweanor 2001; 2.2, Ross and Jalkotzy 1992). As discussed above (see results), insufficient data made it necessary to estimate other parameters involved in maternity rates (interbirth interval, age at first litter, proportion of successful reproducing females) from literature. Because the elasticity value of maternity rate was relatively low (0.19), uncertainties in fecundity values had a negligible influence on population projection results.

Survival rates indicated this cougar population was very heavily hunted (92% deaths of radio-collared cougars) compared to other populations (5%, Logan and Sweanor 2001; 15%, Logan et al. 1986; 35%, Spencer et al. 2001). The overall

survival (0.58) was similar to that encountered in Arizona (0.62, Cunningham et al. 2001). Survival rate of adult females (0.77) was similar to those of other cougar populations (0.82, Logan and Sweanor 2001; 0.77, Lopez-Gonzalez 1999; 0.77 for all adults, Spencer et al. 2001), and higher than the 0.67 reported by Cunningham et al. (2001). Adult male survival (0.33) was much lower than in other areas (0.58, Cunningham et al. 2001; 0.91, Logan and Sweanor 2001; 0.62, Lopez-Gonzalez 1999). Similarly, kitten and yearling survival rates were lower than most rates reported in literature. Kitten survival (0.57) was below 0.72 (Hemker et al. 1986) and 0.76 (Robinette 1961) previously reported, but similar to rates encountered New Mexico (0.59 to 0.63, Logan and Sweanor 2001) and Utah (0.42 for cubs until dispersal, Lopez-Gonzalez 1999). Yearling survival rate (0.34) was lower than previously reported (0.56 and 0.88 for subadult males and females, Logan and Sweanor 2001; 0.60 and 0.80 for juvenile males and females, Spencer et al. 2001).

The elasticity of adult female survival outweighed that of any other parameter, highlighting the large influence of adult female survival on population growth, and minimizing the effect of uncertainties for other parameters that had smaller sample sizes and larger standard deviations.



### **Population growth rate and viability**

The observed declining trend in annual density ( $12 \pm 16\%$ ) corresponded to the decline indicated by the stochastic ( $20 \pm 11\%$ ) and deterministic (13%) growth rates. Because the stochastic growth rate incorporates environmental and demographic variability, it is believed to be more realistic than the deterministic growth rate (Caswell 2001, Morris and Doak 2002). The difference between the 2 values in my model ( $\Delta\lambda = 0.07$ ) is probably related to the large magnitude of environmental variation in vital rates ( $SD = 0.17$ ). Regardless of which method was used, both indicated a steeply declining population.

My results are limited by the uncertainties in some of the model parameters and density estimates. However, the very high elasticity value for adult female survival (0.69) and large sample size ( $N = 28$ ) for this parameter indicated that the population would still be declining even if the other parameters were doubled to unrealistic values. Additionally, if my density estimates had been higher, the simulated population trajectories would have reached extirpation after a longer time delay, but the growth rate would not have been affected. A limitation for population projections is the underlying model assumption that all means and standard deviations will remain constant in the future. Emigration from neighboring populations could significantly increase the viability of this population (Beier 1993,

Sweaner et al. 2000), or a very sparse cougar density could trigger a lower hunting effort.

### **Management implications**

My results reject the hypothesis that cougars are at very high densities and are increasing in northeastern WA, southern BC, and northwestern ID. Cougar densities were not higher than reported in most other areas, and the population appears to be declining. The increased level of cougar complaints following 1996 doesn't seem to be due to excessively high densities and growth rates, but could be related to (1) very young age structure of the population caused by heavy hunting; (2) increased human intrusion into cougar habitat; or (3) low level of social acceptance of cougars by local stakeholders.

The conflicts surrounding cougar management in my study area are not uncommon in other regions of North America. Other populations that are believed to be increasing, as suggested by more frequent cougar encounters, could be declining as well. Conducting similar demographic analyses in different geographic areas where complaints are increasing could shed light on this situation. Educational programs, such as the one undertaken in western WA (CAT project, Koehler and

Nelson 2003), might help alleviate the tension presently surrounding cougar management throughout western North America.

Table 1. Average density estimates for cougars in the study area from 1998 to 2003, as defined by the annual composite adult female home ranges (AF HR) and the abundance  $N$  of each demographic class, estimated with the number of captured and monitored animals (Capt.) and the stable age distribution (SAD).

	<b>95% composite adaptive kernel AF HR (km<sup>2</sup>)</b>	<b>Adult females (<math>N</math>) Capt.</b>	<b>Adult males (<math>N</math>) Capt. SAD</b>	<b>Yearlings (<math>N</math>) Capt. SAD</b>	<b>Kittens (<math>N</math>) SAD</b>	<b>Adults /100km<sup>2</sup></b>	<b>Cougars /100km<sup>2</sup></b>
<b>1998-99</b>	1,826	9	4 2.3	2 7.3	11.1	0.67	1.47
<b>1999-00</b>	3,308	13	2 3.3	8 10.6	16.1	0.47	1.21
<b>2000-01</b>	3,582	12	3 3.1	7 9.8	14.9	0.42	1.05
<b>2001-02</b>	4,744	14	3 3.6	5 11.4	17.3	0.36	0.86
<b>2002-03</b>	5,641	17	3 4.4	5 13.8	21.1	0.37	0.85
<b>Average</b>	3,820	13	3 3.3	5.4 10.6	16.1	0.46	1.09

Table 2. Annual survival rates for cougars in the Pacific Northwest (mean (sample size)) for kittens (0-1yr), yearlings (1-2yr), and adult (2-12yr) males and females, from 1998 to 2003.

	<b>1998-99</b>	<b>1999-00</b>	<b>2000-01</b>	<b>2001-02</b>	<b>2002-03</b>	<b>Mean±95%CI</b>
<b>Kittens</b>	NA	0.25 (4)	1 (3)	0.75 (8)	0.43 (7)	0.57±0.21 (21)
<b>Yearlings</b>	1 (2)	0.53 (7)	0.24 (7)	0.17 (5)	0.41 (5)	0.34±0.35 (17)
<b>Adult males</b>	0.21 (3)	0.50 (2)	0.27 (3)	0.26 (3)	1.00 (3)	0.33±0.47 (8)
<b>Adult females</b>	1 (9)	0.90 (12)	0.91 (11)	0.52 (13)	0.76 (16)	0.77±0.20 (28)
<b>Total radio-collared</b>	0.69 (14)	0.76 (21)	0.65 (20)	0.35 (22)	0.77 (23)	0.59±0.20 (52)

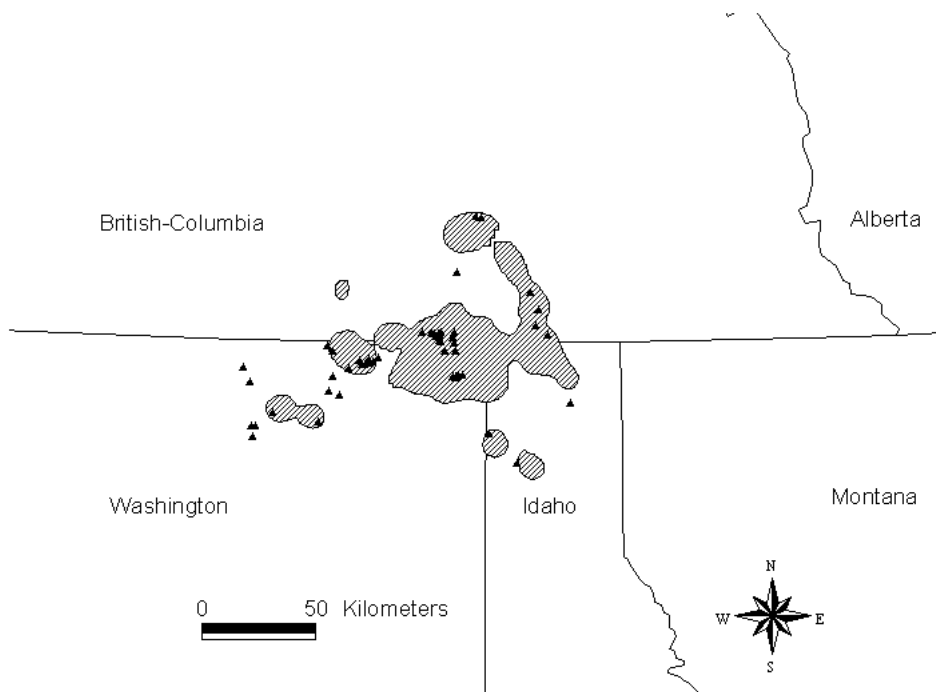


Figure 1. Study area in the Pacific Northwest. The hatched polygons represent the 95% adaptive kernel composite home range of all cougars monitored from 1998 to 2003, and the triangles ( $N = 52$ ) represent capture locations.

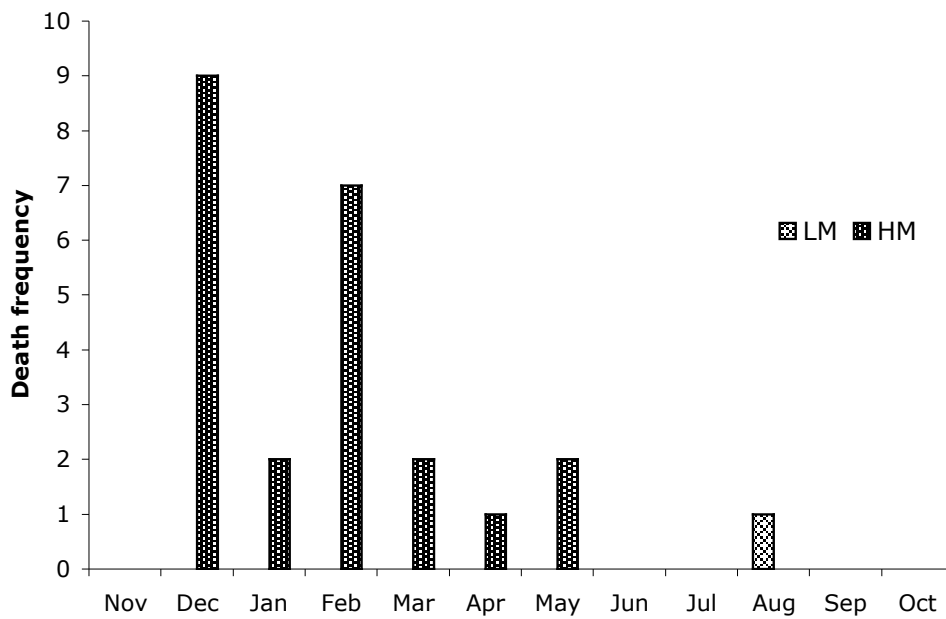


Figure 2. Monthly distribution of the cougar mortalities in the Pacific Northwest, from 1998 to 2003. High mortality (HM) season was from 13 November to 20 May, while the low mortality (LM) season was from 21 May to 12 November. Seasons were defined by the median date of the deaths and were used to meet the assumption of constant mortality within each time interval required by the Heisey-Fuller survival analysis.

	KitF	KitM	YeaF	YeaM	3F	3M	...	11F	11M	F12	M12
KitF	$m_{yf}S_{kf}$	0	$m_{3f}S_{yf}$	0	$m_{4f}S_{3f}$	0	...	$m_{12f}S_{11f}$	0	$m_{13f}S_{12f}$	0
KitM	$m_{ym}S_{kf}$	0	$m_{3m}S_{yf}$	0	$m_{4m}S_{3f}$	0	...	$m_{12m}S_{11f}$	0	$M_{13m}S_{12f}$	0
YeaF	$S_{kf}$	0	0	0	0	0	...	0	0	0	0
YeaM	0	$S_{km}$	0	0	0	0	...	0	0	0	0
3F	0	0	$S_{yf}$	0	0	0	...	0	0	0	0
3M	0	0	0	$S_{ym}$	0	0	...	0	0	0	0
...	...	...	...	...	...	...	...	...	...	...	...
11F	0	0	0	0	0	0	...	0	0	0	0
11M	0	0	0	0	0	0	...	0	0	0	0
12F	0	0	0	0	0	0	...	$S_{11f}$	0	0	0
12M	0	0	0	0	0	0	...	0	$S_{11m}$	0	0

Figure 3. Structure of the Leslie matrix used to model population growth for female and male cougar kittens (KitF, KitM), yearlings (YeaF, YeaM), and adult ( $x$ F,  $x$ M, where  $x$  is the age class from 3 to 12) in the Pacific Northwest, from 1998 to 2003. In the first two rows, fecundity rates ( $F_x$ ) represented the probability that a female of age  $x$  will give birth to a male ( $m_{xm}S_{(x-1)f}$ ) or female ( $m_{xf}S_{(x-1)f}$ ) kitten. The survival rates for kittens ( $S_{kf}$ ,  $S_{km}$ ), yearlings ( $S_{yf}$ ,  $S_{ym}$ ), adult males ( $S_{xm}$ ) and adult females ( $S_{xf}$ ) were the elements of the second-subdiagonal.



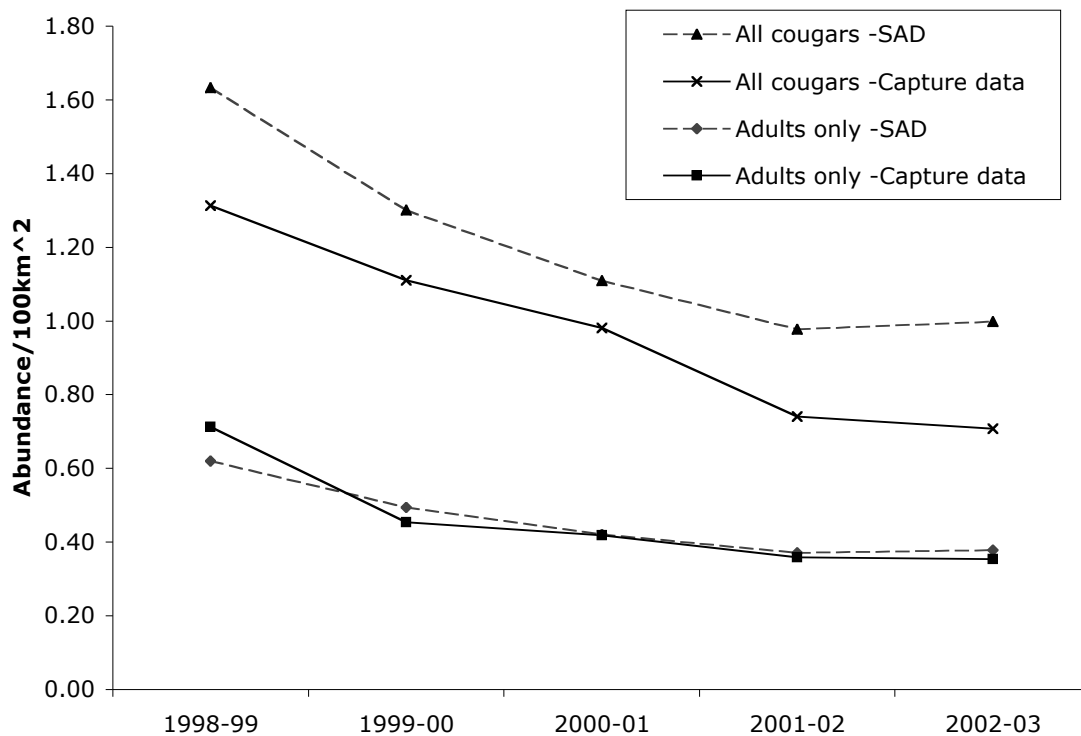


Figure 4. Adult and total cougar density in the Pacific Northwest, from 1998 to 2003, calculated with the 95% composite adaptive kernel home range method for adult females, and projected with both capture data and stable age distribution (SAD) vector to calculate adult male and yearling densities. Kitten density was calculated with the SAD.

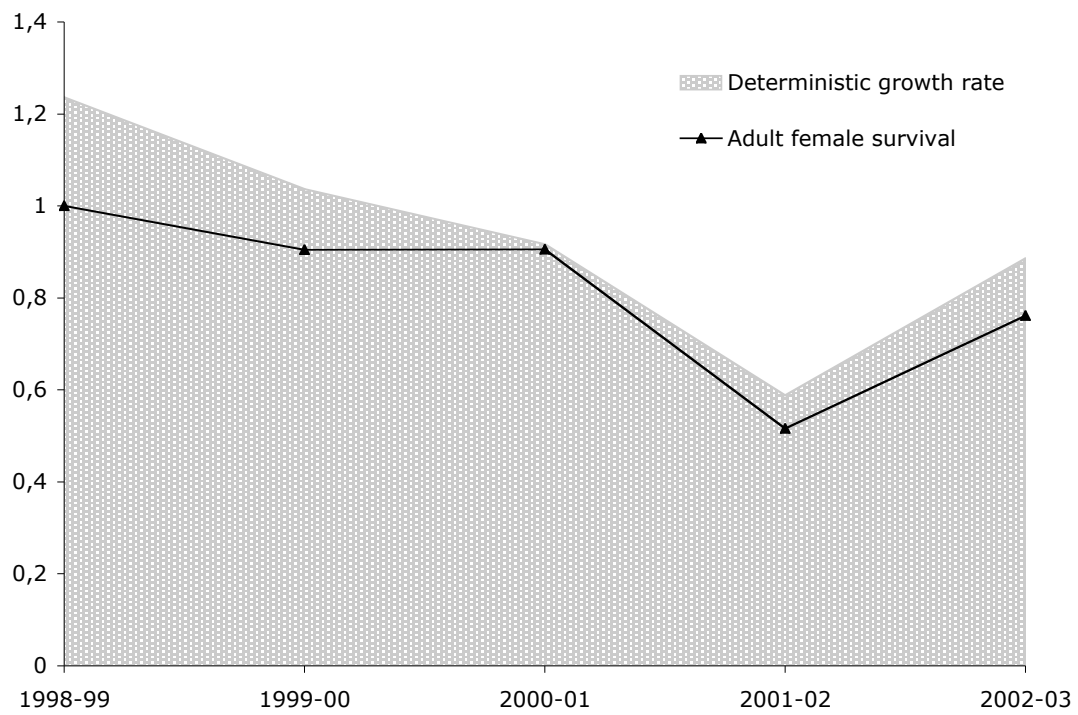


Figure 5. Annual survival rates of adult females and deterministic growth rates  $\lambda_1$  (dominant eigenvalue of annual matrix model), between 1998 and 2003, for cougars in the Pacific Northwest.

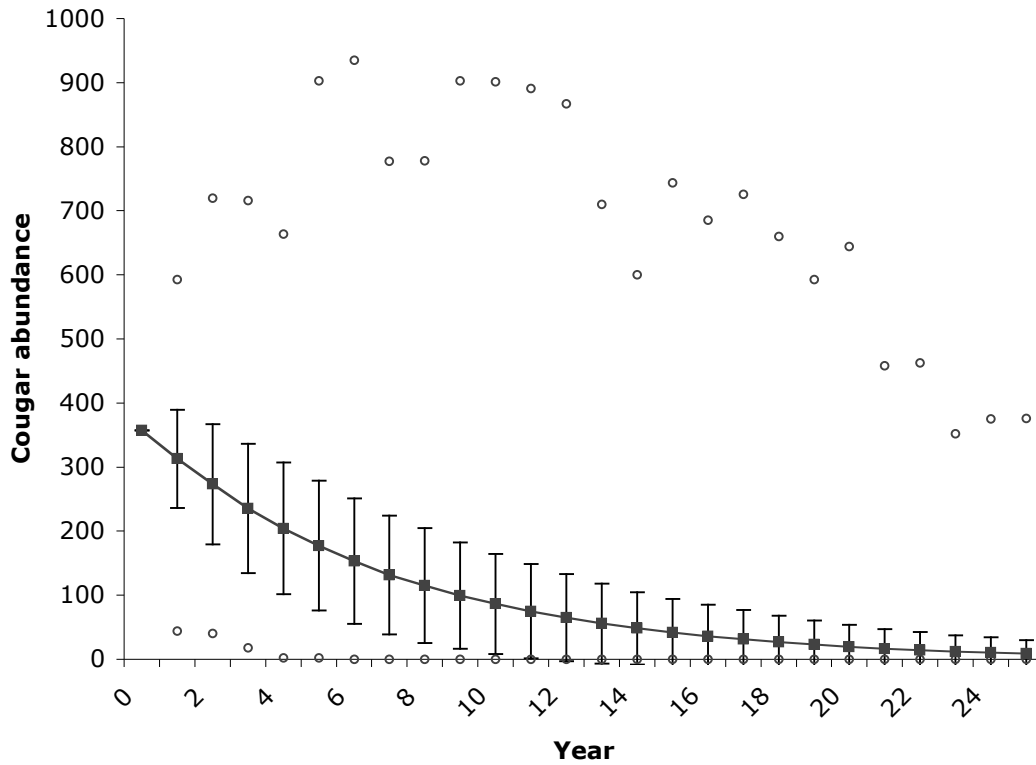


Figure 6. Simulated trajectory of the cougar population in the Pacific Northwest, based on survival and fecundity rates from 1998 to 2003. The squares represent the annual average abundances, the vertical lines are standard deviations, and the empty circles are maximum and minimum values obtained in 5,000 simulations.

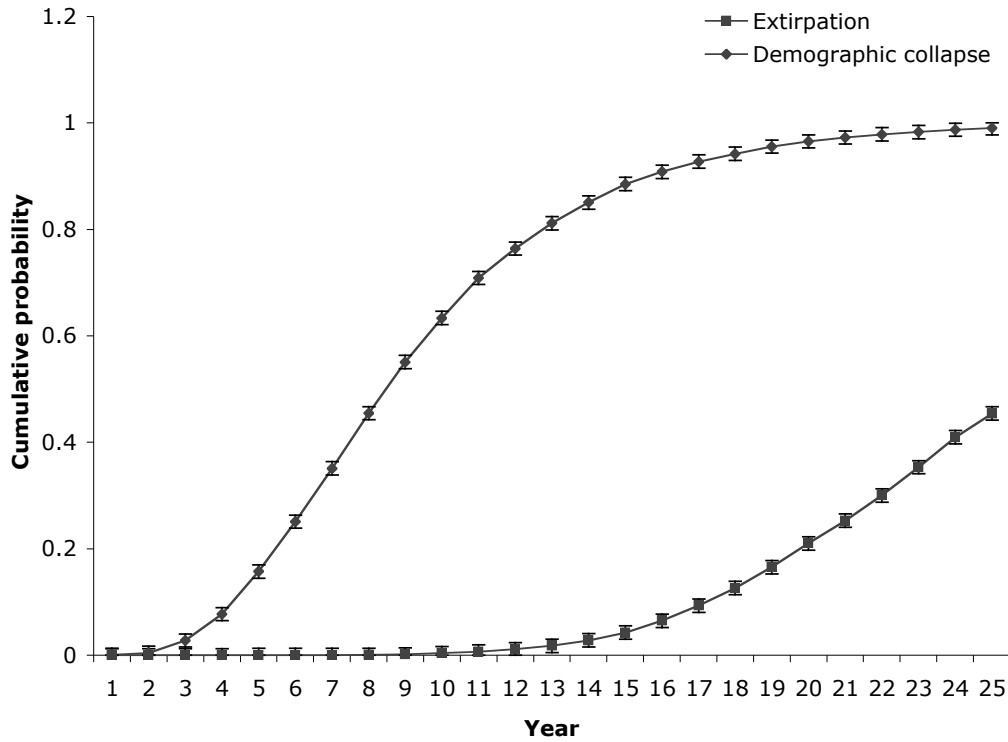


Figure 7. Time to fall from 357 cougars to demographic collapse ( $N = 79$ , equivalent to 30 adults) and extirpation ( $N = 0$ ), based on vital rates estimated for cougars in the Pacific Northwest from 1998 to 2003, and simulated 5,000 times over 25 years.

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