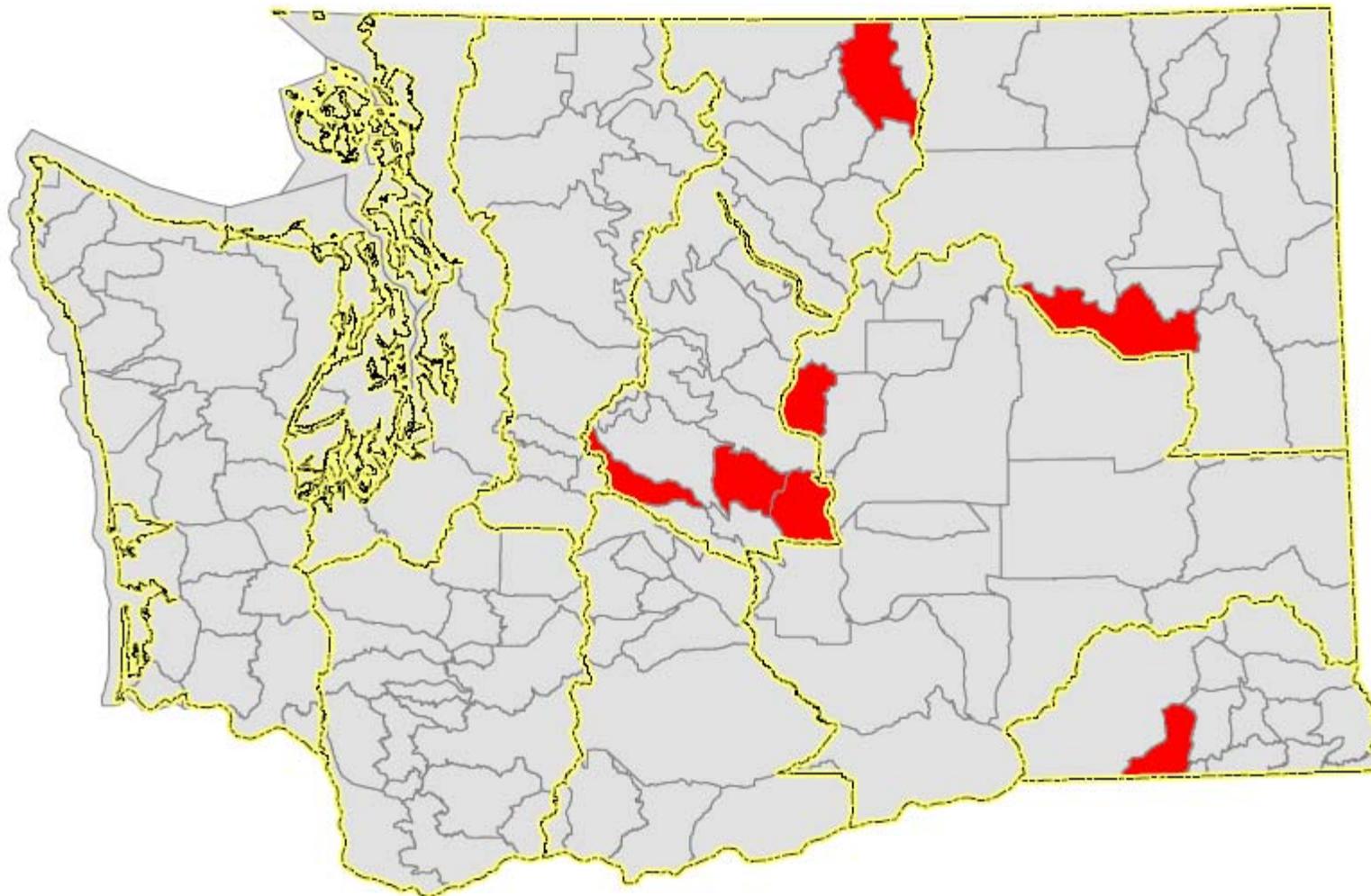


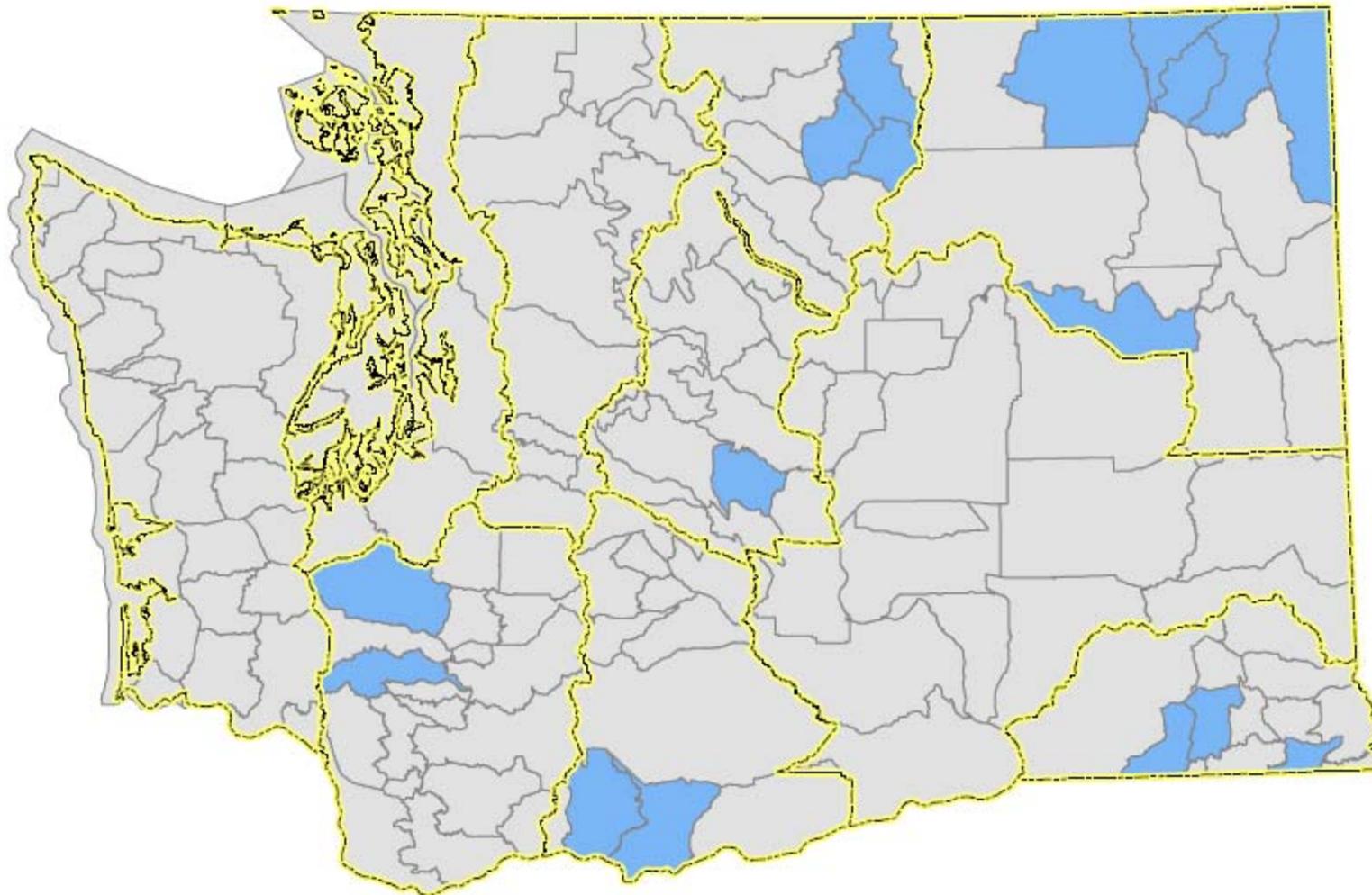
**DRAFT**

GMUs where average adult female harvest (2008-2010) exceeds 14% of estimated adult female density



**DRAFT**

GMUs where average adult male harvest (2008-2010) exceeds 14% of estimated adult male density



# EFFECTS OF TROPHY HUNTING ON FEMALE COUGAR (*Puma concolor*) POPULATION GROWTH AND PERSISTENCE

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## Abstract

Carnivore populations are managed based on the density dependent, compensatory mortality model, which suggests that trophy hunting of males causes an increase in female reproductive success, survival, and population growth. Previous research on cougars showed that increased mortality of males resulted in no net reduction in males due to increased immigration. Female reproduction and survival did not increase with male mortality. That research suggested that female demographics are additive to male mortality and might even be depensatory (inversely compensatory), whereby increased male immigration and infanticide may be associated with decreased female reproductive success, survival, and population growth. In this paper we test the compensatory, additive, and depensatory hypotheses by censoring female hunting deaths and plausible kitten infanticides from two independent cougar populations. The previously observed lack of compensatory demographics allowed us to censor deaths in this manner. The lightly hunted population (male hunting mortality = 0.16) had a female population growth rate of 1.05. With female mortality from hunting removed the growth rate increased to 1.14. The heavily hunted population (male hunting mortality = 0.35) had a female population growth rate of 0.78. With infanticide removed the growth rate increased to 0.89. With hunting mortality of females removed, the growth rate increased to 0.98. With both female mortalities

and infanticide removed, the growth rate increased to 1.14. Light hunting of males (no net male immigration) decreased female population growth in an additive manner and heavy hunting of males (increased net male immigration) decreased female population growth in a depensatory manner. We reject the compensatory mortality hypothesis, and suggest that hunting of males has a negative additive or depensatory effect on female population growth depending on the intensity of male mortality.

Keywords: hunting, cougars, population growth, compensatory mortality, additive mortality, depensatory mortality

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## **1 Introduction**

There are two main hypotheses concerning the effect of hunting mortality on populations: 1) populations compensate for harvest by reduced natural mortality rates and increased reproductive rates (density dependent, compensatory mortality model: Sinclair et al. 2008) and 2) natural mortalities and reproduction remain unchanged regardless of hunting (density independent, additive mortality model: Allen et al., 2006). Both responses have been observed in wildlife populations. For example: Anderson and Bartmann (1976) found that hunting was compensatory in American mallards, *Anas platyrhynchos*, and Staines (1978) and Bartmann et al. (1992) found compensatory effects in mule deer, *Odocoileus hemionus*. On the other hand, Allen et al. (2006) and Dwyer (2009) found additive effects in fish and raptors.

Sport or trophy hunting of herbivores is widely practiced world-wide based on the density-dependent, compensatory mortality model (Staines 1978; Peek 1986; Bartmann et al. 1992) whereby removal of surplus trophy males is expected to be benign or beneficial for females because of increased per-capita resources for females and their offspring. However, there is no compelling

evidence to date to suggest that the compensatory model works in carnivore populations as well (Milner et al. 2007).

Despite little evidence for compensatory mortality in carnivores, managers of grizzly bears (*Ursus arctos horribilis*), cougars (*Puma concolor*), lions (*Panthera leo*), and leopards (*Panthera pardus*) frequently believe that trophy hunting is an effective way to provide hunting opportunities while reducing predation on game animals, depredation on livestock, and human-wildlife interactions; while still maintaining a viable female population (Ross & Jalkotzy 1992, Logan & Sweanor 2001; Caro et al. 2009; Treves 2009). Wielgus and Bunnell (1994a, 1994b, 1995, 1997, 2001), and Swenson et al. (1997, 2003) demonstrated that excessive trophy hunting of resident male North American grizzlies and European brown bears (*Ursus arctos arctos*) corresponded with increased male turnover, increased sexually selected infanticide, and female population decline. Wielgus and Bunnell (1994) called this depensatory population growth (Sinclair et al. 2006). These same depensatory dynamics were later suggested for cougars (Logan & Sweanor 2001, Robinson et al. 2008, Cooley et al. 2009a), tigers (*Panthera tigris*) (Smith & McDougal 1991), lions (Duffy & Packer 1994; Packer et al. 2009, 2010) and leopards, (Caro et al. 2009; Packer et al. 2010).

Cooley et al. (2009) compared a lightly and heavily hunted cougar population while controlling for potential confounding factors such as per capita kill rates and predator density. They found that increased hunting of males did not decrease male densities (due to rapid replacement by immigrants) and that increased male and female hunting deaths did not correspond with increased female reproduction and decreased female natural mortalities. They concluded that hunting was additive not compensatory. In this investigation we go further to test if male mortality is depensatory (the inverse of compensatory: Sinclair et al. 2006) in the same two populations. If cougar populations follow the density-dependent, compensatory mortality hypothesis we would expect to see higher

female reproductive success, natural survival, and population growth as male survival decreases. If cougar populations follow the density-independent, additive mortality hypothesis we would expect to see no net change in female reproductive success, natural survival, and population growth as male survival decreases. If cougar populations follow the inversely density-dependent, compensatory mortality hypothesis we would expect to see lower female reproductive success, natural survival, and population growth as male survival decreases.

To test these hypotheses we modeled a heavily hunted, HH, (hunting mortality rate of males = 0.35) and a lightly hunted, LH, (hunting mortality rate of males = 0.16) cougar population - by removing the effects of hunting (censoring female hunting deaths and plausible infanticides) and recalculating fecundity, kitten survival, juvenile survival, adult survival, and population growth for the female segments of the populations. Because of the additive, non-compensatory effects demonstrated by Cooley et al. (2009) we were able to censor female hunting mortalities and putative kitten infanticides in this manner. We then compared baseline population growth rates with the new rates obtained from the censored data. By simulating the removal of hunting related mortalities we also calculated the intrinsic growth rates (Sinclair et al, 2006) for these two cougar populations.

## **2 Study Areas**

We monitored cougar populations in two study areas >250 km apart. Males were the primary targets of hunting in both areas -- females that are obviously accompanied by kittens (spotted kittens  $\leq$  1 year old) are protected from hunting in Washington. The lightly hunted population had a male hunting mortality rate of 0.16, a net emigration rate (mostly males) of 0.12, an observed growth rate of 0.98, a density of 3.62 cougars/100 km<sup>2</sup>, and a kill rate of 7.04 days between ungulate kills (White 2009). The heavily hunted population had a male hunting mortality rate of 0.35, a net immigration rate (mostly males) of 0.11, an observed growth rate of 0.91, a density of 3.46 cougars/100 km<sup>2</sup>, and a

kill rate of 6.68 days between ungulate kills (Cooley et al. 2009). No differences in prey or predator densities that could bias survival or population growth were observed (Cooley et al. 2009).

### 2.1 Lightly hunted area

This study area was located near the town of Cle Elum along the East-slope foothills of the North Cascade Mountains in Central Washington State. The area includes a portion of the upper Yakima River watershed and covers 594 km<sup>2</sup>. The study area is bounded by the Enchantment Wilderness to the north, the Cascade Mountains on the west and agricultural lands of the Kittitas Valley on the south and east. Predominate vegetation below 550 m is sagebrush steppe, transitioning upward to ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga mensiesii*) forests. At above 1500 m subalpine fir (*Abies lasiocarpa*) Engelmann spruce (*Picea engelmannii*) silver fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) dominate. Precipitation averages 56.4 cm/yr, with 160 cm of snowfall during winter. The mean annual temperature ranges from -7°C in January to 27°C in July. Elk (*Cervus canadensis*) and mule deer are found throughout the study area, with mountain goats (*Oreamnos americanus*) present at higher elevations. Common predator species aside from cougars include black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*).

### 2.2 Heavily hunted area

This study area lies north of the town of Kettle Falls in Northeast Washington State and includes a mix of federal, state, and privately owned land and covers 735 km<sup>2</sup>. The study area is bounded by the Columbia and Kettle Rivers to the southeast and southwest. The northern boundary is formed by the Canada-United States border. The study area is part of a mountainous region (400-2130 m) known as the Okanagon Highlands, and occupies the transition between the Northern Rocky Mountain physiographic province and the East-slope Cascades. Dominant tree species include

Douglas-fir (*Pseudotsuga mensiesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the annual precipitation falls as snow, with an average of 136 cm falling from mid-November to mid-April annually. Mean annual temperatures range from -6°C in January to 21°C in July. White-tail deer (*Odocoileus virginianus*) are the most common ungulate in the study area, but mule deer, elk, and moose (*Alces alces*) are also present. Common predator species aside from cougars include black bears, coyotes, and bobcats.

### **3 Methods**

#### *3.1 Capturing and Monitoring*

From January 2002 through December 2007 we attempted to capture and mark all cougars each year by conducting thorough and systematic searches of each study area during winter when tracks could be detected in the snow. We used hounds to track and tree cougars (Hornocker 1970). Cougars were treed and then immobilized using 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 & Jalkotzy 1992; Speadbury et al. 1996). Sex was determined and animals were classified as kittens (0-12 months), juveniles (13-24 months), or adults (25+ months) based on gum regression measurement of the canine teeth and physical measurements (Laundre et al. 2000).

Each animal was fitted with a mortality-sensing Very High Frequency radio-collar (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA) or Global Positioning Systems radio-collar (GPS; Lotek Wireless, Newmarket, Ontario Canada and Televilt, Lindesberg, Sweden). Starting in January 2005 den sites of collared females were investigated and kittens were captured by hand. Kittens less than 6 weeks old were implanted with PIT (Passive Integrated Transponder) tags (AVID,

Norco, California, USA), and kittens older than 6 weeks old were collared with expandable VHF, very high frequency (Telonics, Mesa, Arizona, USA; T. Ruth, *personal communication*) radio collars to accommodate growth. All animals were handled 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. Data were retrieved using a remote communication unit. Location coordinates of VHF-collared animals were recorded at 1-week intervals from ground or aerial telemetry.

### 3.2 Survival

Radio telemetry was used to monitor survival of all radio-collared cougars. The cause of mortality was assigned as hunting or natural/other. Natural mortalities, such as old age, disease, or starvation were confirmed with necropsies. The putative causes of kitten mortalities were determined by examining the carcass for tooth punctures and close proximity of collared males at the estimated time of death. There were three cases (litters) of plausible infanticide found. From one of the cases 2 kittens were known to have died of predation within 1-2 days in close proximity (< 1km) to a collared male, the 4 kittens from the other 2 cases had obvious evidence of being preyed upon (tooth puncture marks etc.).

The modified Mayfield method (Heisey & Fuller 1985) was used to estimate survival of animals because it provides increased precision and accuracy when sample sizes are small (as is the case here, Winterstein et al. 2001; Murray 2006). Annual survival rates for female and male kittens, female and male juveniles, and adult females were calculated from January 2002 to December 2007. Survival rates were calculated for pooled female and male kittens and pooled female and male juveniles because sample sizes for these age classes were very small and neither sex can be differentiated by hunters at that age (no accompanying kittens). This suggests that hunting mortality

for male and female juveniles should be approximately equal for these age classes (unlike adult females, which are protected from hunting when accompanied by kittens).

To determine intervals when survival probabilities were constant, we analyzed the statistical distribution of deaths over a 365-day period (Lambert et al. 2006). This gave us two mortality seasons: a high mortality season (LH: 1 August to 31 December, HH: 1 October to 31 January), and a low mortality season (LH: 1 January to 31 July, HH: 2 February to 31 September). The product of seasonal survival rates were the annual survival rates (Heisey & Fuller 1985). Intervals were chosen for each period based on the median date of deaths for each period. We used the Taylor series approximation method to compute variances of class-specific survival rate. Binomial z-tests were used to determine if kitten, juvenile, and adult female survival rates differed among areas (LH vs. HH) and modeled (hunting, no hunting) populations (Micromort version 1.3; Heisey & Fuller 1985).

To calculate how survival and population growth changed with hunting, female hunting deaths and plausible kitten infanticides were removed from the original data of Robinson et al. (2008) and Cooley et al. (2009), by reclassifying them as censored animals at the time of death. The new survival parameters (including fecundity  $F_x = S_x * M_x + I$ ) were entered into RAMAS GIS (Akçakaya 2002) to estimate population growth. The 1<sup>st</sup> model used the original data collected by Robinson et al. (2008) and Cooley et al. (2009) which included known female hunting deaths and plausible infanticides. The 2<sup>nd</sup> model removed female hunting mortalities by subtracting these deaths and reclassifying them as censored (e.g., the new survival rates were calculated by adding the female hunting mortality to the survival rates of females). The 3<sup>rd</sup> model removed both female hunting mortalities and plausible kitten infanticides. The 4<sup>th</sup> model removed infanticides only.

### 3.3 Maternity and Fecundity

Maternity rate ( $M_x$ ) was calculated as the mean number of kittens found from snow tracking and inspection of maternal dens, divided by the number of adult females observed through snow tracking and captured that year. Fecundity rates were calculated using the equation  $F = (S_f \times M_{x+1})/2$  (Ebert 1999). For details see Cooley et al. (2009).

### 3.4 Deterministic and stochastic growth rates

A survival/fecundity Leslie matrix for females was constructed to model closed-population growth for each area using RAMAS GIS (Akçakaya 2002). The age of first reproduction for females was set at 24 months, with an equal sex ratio (Lambert et al. 2006). The age of senescence or the maximum age was set at 13 years since this is the age at which female cougars are no longer able to reproduce and few cougars survive past 13 years of age (Robinson et al. 2008). The population was projected for 13 years (12 transitions) to cover a cougar lifespan (Cooley et al. 2009). The initial populations were calculated and set to 21 females for LH and 25 females for HH based on the observed densities of cougars in each area (Cooley et al. 2009) and projected to an average sized game management unit (GMU) for both study areas: GMUs 105 (Kelly Hill), 336 (Taneum) and 335 (Teanaway). The deterministic growth rates were calculated by RAMAS GIS for each of the 4 models.

To calculate the stochastic growth rates each model was projected 100 times, with the initial population and final population recorded. To calculate the mean annual growth rate for each 13 year run we used the equation  $N_0/N_{13}^{1/13}$ , and calculated the arithmetic average and standard deviation of the 100 runs. We used a t-test to compare mean stochastic growth rates among areas (LH vs. HH) and models (hunted vs. un hunted) in each area.

The stochastic growth rate was calculated by incorporating annual environmental and demographic variability. For environmental stochasticity in population projections, we used the standard deviations of annual survival from all cougars (HH = 0.09, LH = 0.06) and standard deviations of annual fecundity (HH = 0.25, LH = 0.27) from Cooley et al. (2009). For demographic stochasticity the number of survivors in each sex and age class was sampled from a binomial distribution, and the number of kittens born each year was sampled from a Poisson distribution using the random number generator in RAMAS GIS (Akçakaya 2002).

### *3.5 Elasticity*

We used elasticity analysis to compare the relative effects of changes in age-specific survival or fecundity on population growth (Sinclair et al. 2006), thus determining which life stages are most important for population growth. We calculated elasticities for juvenile fecundity, adult fecundity, kitten survival, juvenile survival, and adult survival using RAMAS GIS. Elasticities for adult survival and fecundity are based on averages for adult females 3-12 years old.

## **4 Results**

### *4.1 Mortality and Survival*

We captured and monitored 103 cougars in the two study sites (57 in HH and 46 in LH) from January 2002 to December 2007. During our study 53 radio-collared cougars died (35 in the HH, 18 in the LH, Table 1). Hunters killed 26 cougars (9 females), 22 died from natural causes (12 females), 3 died in vehicle collisions (1 female) and 2 were killed from depredation hunts (1 female). Of the 42 radio-collared kittens, 18 survived to 1 year (juvenile age class), 16 died from natural causes and 4 were censored from each area (8 total). Six of the 16 natural kitten mortalities (3 females, 2 males, 1 unknown sex) were classified as plausible infanticides in the HH based on proximity of males and/or evidence of predation (Cooley et al 2009).

Table 1. Mortality rates of radio-collared female cougars in the heavily hunted (HH) and the lightly (LH) hunted study areas of Washington from 2002-2007.

Sex and Age	(HH)			(LH)		
	n	Hunting	Natural/other	n	Hunting	Natural/other
Kitten <sup>a</sup>	23	0.00 ± 0.00	0.69 ± 0.18	19	0.00 ± 0.00	0.42 ± 0.17
Juvenile <sup>b</sup>	18	0.31 ± 0.12	0.07 ± 0.00	13	0.23 ± 0.21	0.15 ± 0.13
F Adult <sup>c</sup>	19	0.22 ± 0.07	0.12 ± 0.06	12	0.04 ± 0.04	0.09 ± 0.06

Note: Sample sizes (n = total number of animals at risk), mortality rates (mean ± SD)

<sup>a</sup> 0-12 months      <sup>b</sup> 13-24 months      <sup>c</sup> 24+ months

With hunting and infanticide included, adult females had a significantly higher survival rate ( $Z = 7.143$ ,  $P < 0.0001$ ) in the LH (0.87) than in the HH (0.66) (Tables 2 and 3). Survival of kittens was also higher in the LH (0.58 vs. 0.31,  $Z = 8.26$ ,  $P < 0.0001$ ), but there was no difference in survival of juveniles between areas (0.62 vs. 0.62,  $Z = 0$ ,  $P = 1.00$ ). After removing the effects of hunting (female deaths) and plausible infanticide, survival rates were remarkably similar for the 2 populations (S kitten = 0.59 vs. 0.58, S juvenile = 0.93 vs. 0.85, S adult = 0.88 vs. 0.92) with only a significant difference in juveniles ( $Z = 2.0$ ,  $P = 0.0455$ ).

In the HH there was a significant increase in survival for adult females (0.88 vs. 0.66,  $Z = 3.4$ ,  $P = 0.0007$ ), juveniles (0.93 vs. 0.62,  $Z = 5.4$ ,  $P < 0.001$ ), and kittens (0.59 vs. 0.31,  $Z = 4.2$ ,  $P < 0.0001$ ) after removing hunting mortalities and plausible infanticides. In the LH only juveniles showed a significant increase in survival (0.85 vs. 0.62,  $Z = 2.4$ ,  $P = 0.0164$ ) after hunting was removed.

Table 2. Survival rates of female cougars for each of the 4 models in the heavily hunted study area in Washington from 2002-2007. Model 1: with hunting and infanticide included, Model 2: with hunting deaths removed, Model 3; with hunting and infanticide removed, and Model 4: with infanticide removed.

Sex and Age	n	Model 1	Model 2	Model 3	Model 4
Kitten <sup>a</sup>	23	0.31 ± 0.10	0.31 ± 0.10	0.59 ± 0.10	0.59 ± 0.10
Juvenile <sup>b</sup>	18	0.62 ± 0.06	0.93 ± 0.06	0.93 ± 0.06	0.62 ± 0.06
F Adult <sup>c</sup>	19	0.66 ± 0.08	0.88 ± 0.08	0.88 ± 0.08	0.66 ± 0.08

Note: Sample sizes (n = total number of animals at risk), survival rates (mean ± SD)

<sup>a</sup> 0-12 months      <sup>b</sup> 13-24 months      <sup>c</sup> 24+ months

Table 3. Survival rates of female cougars for each of the 2 models in the lightly hunted study area in Washington from 2002-2007. Model 1: with hunting included, Model 2: with hunting deaths removed.

Sex and Age	n	Model 1	Model 2
Kitten <sup>a</sup>	19	0.58±0.11	0.58 ± 0.11
Juvenile <sup>b</sup>	13	0.62 ± 0.12	0.85 ± 0.12
F Adult <sup>c</sup>	12	0.87 ± 0.08	0.91 ± 0.08

Note: Sample sizes (n = total number of animals at risk), survival rates (mean ± SD)

<sup>a</sup>0-12 months      <sup>b</sup>13-24 months      <sup>c</sup>24+ months

#### 4.2 Maternity and Fecundity

Mean litter size was  $2.63 \pm 0.80$  (n=18 litters) in HH and  $2.47 \pm 0.83$  (n=15 litters) in LH (Cooley et al. 2009). Mean maternity rate was 1.15 kittens/female/year in HH and 1.12 kittens/female/year in LH. Fecundity rates in the 1<sup>st</sup> model with hunting deaths and infanticide were 0.38 in HH and 0.46 in LH. After removing effects of hunting the fecundity rates were the same for the 2 populations at 0.51 in HH and 0.51 in LH.

#### 4.3 Population Growth

##### 4.3.1 Comparing areas:

For baseline Model 1 (with hunting deaths and infanticide included) the deterministic annual female growth rates were 0.80 in HH and 1.05 in LH. The stochastic growth rates (mean  $\lambda \pm$  SD) were  $0.78 \pm 0.11$  in HH and  $1.05 \pm 0.01$  in LH. The difference in stochastic growth rates between areas ( $1.05 - 0.78 = 0.27$ ) was significant ( $t = 12.27, P < 0.0001$ ). For Model 2 (without deaths of females but including infanticide), the deterministic growth rates were 0.99 in HH and 1.14 in LH. The stochastic growth rates were  $0.98 \pm 0.04$  in HH and  $1.14 \pm 0.03$  in LH. The difference ( $1.14 - 0.98 = 0.16$ ) was significantly different at  $t = 22.2, P < 0.0001$ . For Model 3 (without hunting deaths and infanticide) the deterministic growth rate was 1.13 in HH and 1.14 in LH. The stochastic growth rates were  $1.14 \pm 0.01$  in HH and  $1.14 \pm 0.03$  in LH. There was no significant difference for Model 3

between areas ( $1.14 - 1.14 = 0.00$ ,  $t = 0$ ,  $P = 1.0$ ). In Model 4 (without infanticide but with hunting deaths of females included) the deterministic growth rate was 0.89 in the HH and baseline 1.05 in the LH. The stochastic growth rates were  $0.89 \pm 0.17$  in the HH and baseline  $1.05 \pm 0.01$  in the LH. There was a significant difference for Model 4 between areas  $1.05 - 0.89 = 0.16$ ,  $t = 4.69$ ,  $P < 0.0001$ ). In both populations, the intrinsic growth rates were identical at 1.14 when the effects of hunting were removed.

#### *4.3.2 Comparing models:*

In the LH there was a significant difference ( $t = 13.04$ ,  $p < 0.0001$ ) in female population growth due to hunting mortalities (e.g., Model 2 – Model 1,  $1.14 - 1.05 = -0.09$ ). In the HH there was also a significant difference ( $t = 7.35$ ,  $P < 0.0001$ ) in growth rate due to hunting mortalities (Model 3 – Model 4,  $1.14 - 0.89 = -0.25$ ). There was a significant difference ( $t = 19.51$ ,  $P < 0.0001$ ) in growth rate due to plausible infanticide (Model 3 – Model 2,  $1.14 - 0.98 = -0.16$ ). Finally, there was a significant difference ( $t = 16.29$ ,  $P < 0.0001$ ) due to combined hunting mortalities and infanticide (Model 3 – Model 1,  $1.14 - 0.78 = -0.36$ ).

#### *4.4 Population Persistence*

In the HH, with all hunting effects included, the probability of the female population ( $N=25$ ) reaching extinction ( $N=0$ ) in 13 years was 68.3%. With hunting and infanticide removed the risk dropped to only 0.2%. In the LH, with hunting included, the probability of the population reaching extinction ( $N=0$ ) was 4%. With hunting removed the risk dropped to only 0.2%.

#### *4.5 Elasticity*

In both populations, survival of kittens or plausible infanticide effects showed the largest elasticity for any single age class, followed by juvenile survival, juvenile fecundity, average adult

survival and average adult fecundity (Tables 4 and 5). The elasticities for all parameters were similar between both the lightly hunted and heavily hunted populations.

Table 4: Elasticity for female cougars for each of the 2 models in the lightly hunted (LH) study area in Washington from 2002-2007. Model 1: with hunting included, Model 2: with hunting deaths removed.

Stage Class and parameter	Model 1	Model 2
Kitten Survival	0.20	0.20
Juvenile Survival	0.15	0.16
Juvenile Fecundity	0.05	0.05
Average Adult Survival	0.05	0.05
Average Adult Fecundity	0.015	0.015

Table 5: Elasticity of female cougars for each of the 4 models in the heavily hunted (HH) study area in Washington from 2002-2007. Model 1: with hunting and infanticide included, Model 2: with hunting removed, Model 3; with hunting and infanticide removed, and Model 4: with infanticide removed.

Stage Class and parameter	Model 1	Model 2	Model 3	Model 4
Kitten Survival	0.19	0.18	0.23	0.21
Juvenile Survival	0.15	0.15	0.17	0.16
Juvenile Fecundity	0.04	0.03	0.06	0.05
Average Adult Survival	0.05	0.06	0.04	0.05
Average Adult Fecundity	0.015	0.015	0.017	0.016

## 5 Discussion

Our results reject the compensatory mortality hypotheses, because fecundity, kitten survival, juvenile survival, adult female survival, and female population growth rate did not increase with increasing male hunting mortality. LH shows evidence of additive mortality because adult female mortalities were hunting related. However, our results show that it is more than additive mortality in the HH, it is depensatory. Fecundity, natural (non-hunting) kitten survival, juvenile survival, adult female survival, and female population growth did not remain similar with increasing male mortality in the HH - indirect (non-hunting) kitten mortalities (plausible infanticides) actually increased in the HH.

Overall, our results support the depensatory mortality hypothesis because fecundity, indirect natural kitten survival, juvenile survival, adult female survival, and female population growth decreased with increasing male hunting mortality in the HH. The high hunting (mortality rate= 0.36) of male cougars appears to have a significant negative effect on female population growth and persistence because of increased hunting deaths of females (additive deaths) and plausibly increased infanticide (depensatory deaths).

We showed that additive female mortalities reduced population growth by 0.25 (from 1.14 to 0.89) in the HH. Female survival has traditionally been assumed to increase when males were removed based on compensatory mortality; however, the data from this study shows a large decrease in female survival in the HH. Our data showed that with hunting removed, adult female survival increased by 22%. In the LH area female survival also increased with the removal of hunting, though the change was not as great with an increase of only 5%. Although cougars were targeted by hunters in both areas (35% male hunting mortality vs. 16% for females in HH, 16%

for males vs. 5% for females in the LH, Cooley et al. 2009), the hunting mortality of females was still large enough to cause female population declines in the HH (1.14 vs. 0.89, this paper).

Looking at adults only, males suffered a 46% hunting mortality rate in the HH compared to 16% for adult females. Adult males suffered a 16% hunting mortality rate in the LH compared to 7% for adult females. That corresponds to an approximate 3 times higher hunting mortality for males. However, this large difference between sexes appears to diminish for independent juveniles (though the sample size for this age class was the smallest). Juveniles showed an even larger increase in survival when hunting was removed, though the juvenile sample size was small (+31% in the HH, + 23% in the LH). The hunting mortality rates for adult males were similar to that of juveniles in both areas (HH = 46% vs 31%, LH = 16% vs. 23%), perhaps because hunters cannot differentiate sex at that age (e.g., no accompanying kittens to allow discrimination).

Our most surprising result was the relatively large negative effect of plausible infanticide. We showed that depensatory infanticide alone reduced population growth by  $1.14 - 0.98 = -0.16$  in the HH. The corresponding highest elasticity (0.19 – 0.23) for kitten survival also pointed to the fact that survival of kittens is very important for female cougar population growth. Although total adult elasticity (all age classes) did account for 65% of the total population growth, elasticity of kitten survival was 4 times larger than the elasticity for any other single age class of female survival. Even if there were no additive female hunting deaths, the HH cougar population may still decline ( $0.98 \pm 0.04$ ) because of depensatory infanticide alone.

It could be that the significantly decreased survival of kittens due to predation in the HH ( $0.59 - 0.31 = -0.28$ ) was actually due to some other, as yet unknown natural mortality factor that predisposed kittens to predation. Perhaps the increased predation only appears to be associated

with nearby males at time of death, though this was only found in 1 of the 3 infanticide cases) and increased male immigration in the HH (+0.11/yr, Cooley et al. 2009). But again, once the effects of plausible infanticide were removed, kittens in both populations appeared to have very similar natural survival rates of about 60% - suggesting that there were no other differences accounting for the variable kitten survival. Furthermore, failure to accept increased infanticide as a real phenomenon results in an intrinsic growth rate of only 0.98 in the HH compared to 1.14 in the LH. An intrinsic growth rate of 0.98 seems biologically impossible for an extant species. Accepting increased infanticide as a real phenomenon resulted in intrinsic growth rates of 1.14 in both areas.

Whitman et al. (2004), Caro et al. (2009), and Packer et al. (2009) predicted and later observed (Packer et al. 2010) that trophy hunting of males results in population declines for African lions and leopards – probably due to increased sexually selected infanticide resulting from high male turnover (Packer et al. 1988). Swenson et al. (1997, 2001a, b) and Swenson (2003) observed the same phenomenon in European brown bears. Male carnivores are known to kill unrelated young to induce estrous in females (Smith & McDougal 1991; Ross & Jalkotzy 1992; Pusey & Packer 1994; Swenson et al. 1997; Logan & Sweanor 2001; Swenson 2003; McLellan 2005). During our study there were 6 plausible infanticides in the HH. This could be due to the higher male mortality (35%/yr) and higher turnover in the HH (net male immigration rate was +13%/yr) compared to the lower male mortality (16%) and much lower male turnover in the LH (net male emigration rate was -12%/yr) (Cooley et al. (2009).

Originally, Cooley et al. (2009) suggested cougars responded to hunting under the additive mortality model. However, our results go further, suggesting that heavy hunting results in a decrease in adult female and kitten survival as male mortality decreases. Increased male

mortality in the HH was compensated by male immigration. Long-distance dispersal is common in cougar populations (Stoner et al. 2006) helping to maintain populations by replacing mortalities with dispersing animals from neighboring areas. Because male cougars are the dispersers (Sweaner et al. 2000), male populations remain stable or even increase (Robinson et al. 2008) as hunting pressure goes up, while the female population simultaneously decreases (Robinson et al. 2008; Cooley et al. 2009).

Not only does the high hunting levels of male cougars reduce female survival and growth rates, but it was also shown to reduce the persistence of the cougar populations in the HH. The HH probability of extinction dropped from 68.28% to 0.2% when hunting was removed. Once hunting is removed both HH and LH populations show very similar persistence data with only about 0.2% of reaching extinction, because the cougar numbers (25 vs. 21) and intrinsic growth rates (1.14) were similar in both areas.

Heavy hunting resulted in a female population decline (0.89) due to hunting mortalities, a smaller (though still significant) female population decline (0.98) due to plausible infanticide, and a very severe female population decline (0.78) due to the combined effects of hunting mortalities and infanticide. By contrast, light hunting resulted in a slightly increasing female population ( $1.05 \pm 0.01$ ). It appears that hunting mortality rates in excess of the intrinsic rate of increase (1.14) causes female population declines. Male hunting mortality rates equal to or less than the intrinsic rate of increase ( $\leq 14\%$ ) should allow sustainable harvests but rates in excess of 14% appears to result in compensatory population decline.

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Table 1. Percent of female quota harvested by Dec 1 (data from seasons where cougar season overlapped with modern deer season). On average, 54% of the female quota is reached by Dec 1 when cougar season overlaps with modern deer season.

Season	ZONE					Average
	Chelan	Okanogan	Ferry-Okanogan	Stevens-Pend Oreille	Klickitat	
2004-05	50%	82%	30%	33%	--	49%
2005-06	0%	64%	10%	27%	--	25%
2006-07	75%	55%	40%	53%	--	56%
2007-08	100%	45%	90%	73%	--	77%
2008-09	50%	71%	33%	67%	100%	64%
						54%