

# Source populations in carnivore management: cougar demography and emigration in a lightly hunted population

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## Keywords

carnivore; cougar; hunting; emigration; mortality; survival; population dynamics; population growth rate.

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## 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, such a closed population structure may not be an appropriate model for management of carnivore populations where immigration and emigration are important population parameters. The 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 hunting mortality may not result in more carnivores because of compensatory emigration. Previous research supported the open population hypothesis with high immigration rates in a heavily hunted (hunting mortality rate = 0.24) cougar population in northern Washington. We test the open population hypothesis and high emigration rates in a lightly hunted (hunting mortality rate = 0.11) cougar population in central Washington by monitoring demography from 2002 to 2007. We 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 closed survival/fecundity growth rates of 1.13 (deterministic) and 1.10 (stochastic), and suggests a 12–15% annual emigration rate. Our data support the open population hypothesis for lightly hunted populations of carnivores. Low hunting mortality did not result in increased numbers and densities of cougars, as commonly believed because of compensatory emigration.

## 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 & Robinson, 2003; Sinclair, Fryxell & Caughley, 2006) based on the closed population paradigm (e.g. increased deaths = decreased numbers). 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, based on the same closed population paradigm (Treves & 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 (Strickland *et al.*, 1994; Treves & Karanth, 2003).

Heavy hunting mortality (hunting mortality rate = 0.38/year) over a very large area (32 800 km<sup>2</sup>) did result in a cougar population decline in the Selkirk Mountains of south-

ern British Columbia, northern Idaho and northeastern Washington (Lambert *et al.*, 2006). However wildlife agencies typically manage carnivore numbers in much smaller, localized game management units. Cougar-occupied game management units average 904 km<sup>2</sup> [standard deviation (SD) = 763,  $n = 133$ ] in Washington State, with explicit harvest and management prescriptions for each. The effects of hunting at these smaller scales do not consider the potential influences of immigration and emigration on the outcome of those hunting practices (Cougar Management Guidelines Working Group, 2005: 42–44). Nonetheless, 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 intrinsic dispersal is an important aspect of carnivore population ecology (Chepko-Sade & Halpin, 1987; Howe, Davis & Mosca, 1991; Sweanor, Logan & Hornocker, 2000; Frank & Woodroffe, 2001; Zimmerman,

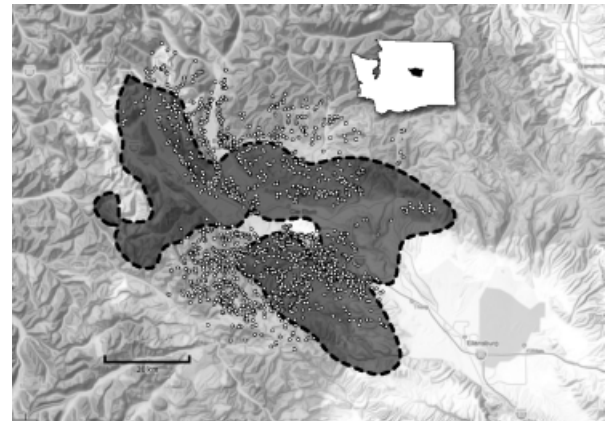
Breitenmoser-Wursten & Breitenmoser, 2005; Whitman *et al.*, 2007). High rates of emigration can depress population growth, and high rates of immigration can increase population growth regardless of birth and death rates. Failure to consider these dynamics may preclude achievement of management objectives for carnivores.

Cougars are hunted for sport and population control throughout the western USA 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 (Ross & Jalkotzy, 1992; Sweanor *et al.*, 2000; Logan & Sweanor, 2001), 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 typically sized (766 km<sup>2</sup>) game management unit (GMU 105) 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 north-east Washington (Robinson *et al.*, 2008).

In this study, we test the open and closed population hypotheses for a lightly hunted (hunting mortality rate = 0.11) cougar population in a typically sized 655 km<sup>2</sup> management area from 2001 to 2007 in central Washington. We compare a closed population growth model based on survival/fecundity rates to open, observed rates of population growth over a 6-year period. We test whether low hunting mortality results in high population growth and increased densities, 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 655 km<sup>2</sup> study area, located on the east slope of the North Cascades near the town of Cle Elum, WA, was composed of a patchwork of public (US 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. The study area was surrounded on three sides by contiguous cougar habitat that did not present a barrier to animal movements (home ranges of several animals straddled the border) (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 south-east. 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



**Figure 1** The central Washington study area showing the study area boundary defined by the 95% composite home range for female cougars *Puma concolor* (dashed line), and male global positioning system points (circles) used to calculate cougar densities. Contiguous cougar habitat and a lack of confining landscape features allow cougar movements to cross study area boundaries.

averages 56.4 cm year<sup>-1</sup>, with the majority falling in winter as snow (average winter snowfall is 160 cm).

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), we used the same methods for all aspects of this study.

### Captures and monitoring

We 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. We used hounds to track and tree cougars in winter (Hornocker, 1970). We immobilized treed cougars with a mixture of ketamine hydrochloride (concentration level: 200 mg mL<sup>-1</sup>) and xylazine hydrochloride (concentration level: 20 mg mL<sup>-1</sup>), at a dosage of 0.4 mL/10 kg of body mass, using a projectile dart in the hindquarter (Ross & Jalkotzy, 1992; Spreadbury *et al.*, 1996). We determined sex by examining visible genitalia and age from measurements of gum regression (Laundre *et al.*, 2000) and assigned age classes as kitten (0–12 months), juvenile (13–24 months) and adult (25+ months).

We fitted each animal with a mortality-sensing very high frequency (VHF, Advanced Telemetry Systems, Isanti, MN, USA) or global positioning system (GPS, Lotek Wireless

Inc., Newmarket, ON, Canada and Televilt, Lindesberg, Sweden) collar. Beginning in January 2005, we investigated den sites of GPS-collared females, and captured kittens by hand. We collared kittens that were >6 weeks old with expandable VHF (Telonics Inc., Mesa, AZ, USA; T. Ruth, pers. comm.) radio collars. We handled all animals in accordance with Washington State University Animal Care (IACUC permit 3133) and Animal Welfare Assurance Committee (permit A3485-01). We recorded locations of VHF-collared animals at 1-week interval from ground or aerial telemetry, and of GPS-collared animals from remote retrieval of 4-h interval satellite location data.

Despite attempts to systematically search and capture animals, we were not able to radio collar the entire population. Therefore, to establish a minimum population estimate we included demographic data from both 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, Wolfe & Choate, 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. We back-calculated the lifespan of each animal to the beginning of the study, its birth date (females) or immigration date (males) as described by Logan & Sweanor (2001: 66), Stoner *et al.* (2006) and Robinson *et al.* (2008). This method reduced chances of missing animals for any given year because the trapping effort is 'cumulative' over time. We did not include the last year of data for observed numbers and densities because animals could not be similarly back-calculated for that year. Because measurements of gum regression and cementum annuli yield comparable ages (Robinson *et al.*, 2008), we included all collared and uncollared animals in a linear regression analysis to examine trends in age structure over the study period.

## Survival

We 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. We inferred cause of kitten mortalities by examining the carcass and proximity to collared cougars.

We calculated age-specific radio days and survival for each collared animal, based on a dynamic year determined by their age at capture. For example, an animal collared in January at an age of 21 months contributed 4 months of radio days to juvenile (13–24 months) survival and was assumed to become an adult (25+ months) in May. We used the modified Mayfield method (Mayfield, 1961; Heisey & Fuller, 1985) to estimate survival of animals because it performs well for small sample sizes, and estimates seasonal and cause-specific mortality rates (Winterstein, Pollock & Bunc, 2001; Lambert *et al.*, 2006; Murray, 2007; Robinson *et al.*, 2008). We estimated mean annual survival rates for male and female kittens, juveniles and adults from 2002 to December 2007. To estimate annual environmental variation, we calculated a weighted average of demographic

variance from pooled sex and age classes and then subtracted it from the total observed variance (Akçakaya, 2002). This estimate minimizes sampling error and accounts for demographic stochasticity.

We 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 (1 August to 31 December) and the low mortality season (1 January to 31 July). Intervals for each period were chosen based on the median date of the deaths for each period. We 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 & Fuller, 1985).

## Maternity and fecundity

We calculated maternity as the mean number of kittens divided by the number of adult females observed that year (Case, 2000). We 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, we calculated a weighted average of demographic variance and then subtracted it from the total observed variance (Akçakaya, 2002). This estimate minimizes sampling error and accounts for demographic stochasticity.

## Deterministic and stochastic growth rates

We 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 (Akçakaya, 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 & Sweanor, 2001).

We calculated the deterministic growth rate ( $\lambda_D$ ) as the dominant eigen value of the matrix under a stable age distribution. We calculated the stochastic growth rate ( $\lambda_S$ ) by incorporating annual environmental variability (SD of annual survival and fecundity rates) and demographic stochasticity. To estimate demographic stochasticity, we 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). We sampled vital rates from a log normal distribution to avoid truncations, which can occur if SD are large due to sampling and measurement error. We projected the population for 6 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

We determined the observed growth rate ( $\lambda_O$ ) from annual counts of collared and unmarked cougars. Each year we tallied the number of cougars (adults, juveniles and kittens)

in the study area, and calculated the observed population growth rate,  $\lambda_O$ , as  $\lambda_x = (n_t/n_0)^{1/t}$  where  $\lambda_x$  is the annual finite growth rate,  $n_0$  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). We used a one-tailed, one-sample  $t$ -test (Zar, 1999) to determine whether deterministic ( $\lambda_D$ ) and stochastic ( $\lambda_S$ ) growth rates were higher than the average 6-year observed ( $\lambda_O$ ) growth rate (Robinson *et al.*, 2008). Standard errors for mean  $\lambda_O$  were based on annual variation of  $\lambda_O$  from 2002 to 2007 ( $n = 5$ ). We estimated emigration rate ( $e$ ) using the equations  $e = \lambda_D - \lambda_O$  and  $e = \lambda_S - \lambda_O$  (Peery, Becker & Beissinger, 2006). We also used observations of radio-collared cougars to document emigration and immigration from 2005 through 2007, the period during which we had accurate kitten survival data.

## Population density

We estimated mean annual density (cougars/100 km<sup>2</sup>) for collared and unmarked cougars present in the core study area from August 2001 through July 2007. The core area was determined by the mean annual composite 95% female home range. Because the core area (655 km<sup>2</sup>) was small (and open) compared with the mean male home range size (416 km<sup>2</sup>), this estimate represented a maximum density, particularly for males. This method provided a consistent measure of density among years and permits comparison with Robinson *et al.* (2008) who used the same methodology, but should not be compared with areas elsewhere. To eliminate the bias associated with large male home ranges that extended beyond the study area boundary, we also calculated density using the proportional number of cougar locations (McLellen, 1989) that fell within the mean annual composite 95% female home range. We calculated the composite range for each year using ArcGIS 9.2 (ESRI, Redlands, CA, USA). We plotted all male and female GPS locations for the corresponding year and calculated the proportion of points within this composite range. We used linear regression to test for significant changes in density over the study period (Zar, 1999).

## Results

### Captures and monitoring

Trained dogs were used as our main method to capture cougars during snow-covered months from January 2002 to December 2007. Those efforts resulted in an average of 84 search days per year (range = 34–136 days) and 44 captured cougars: six female and 13 male kittens, one female and four male juveniles, and eight female and 12 male adults. We also counted 21 unmarked cougars that were shot in the 655 km<sup>2</sup> study area: two female and zero male kitten, two female and three male juveniles, and nine female and five male adults. One uncollared female kitten died from a vehicle collision (Table 1).

### Survival and mortality

Eighteen of 44 radio-collared cougars were killed during the study period. Seven were killed by hunters, three died in collisions with vehicles and six died of natural causes (Table 2). Six juvenile cougars (two females, four males) emigrated out of the study area and we censored these on their last known date in the area. We censored an additional seven animals after they shed their collars or lost VHF signals. We also censored one kitten that died 2 weeks after sustaining an injury during capture. Of 19 radio-collared kittens, nine survived to dispersal age of 18 months (five males, four 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 3). 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 ( $0.65 \pm 0.11$ ,  $Z = 1.71$ ,  $P = 0.08$ ). We did not detect differences among other sex and age classes. We estimated environmental SD 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

We 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 per female per year. The fecundity rate  $F_x$  was  $0.49 \pm 0.22$  kittens of each sex per year. We estimated environmental SD of fecundity at 0.27 female kittens per year. Three female progeny were recruited into the population as adults, and we documented no recruitment from male progeny; all male progeny dispersed.

### 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 the net emigration; we documented six emigrants (two female, four males) and three male immigrants from 2005 to 2007.

**Table 1** Numbers of cougars *Puma concolor* detected (collared and uncollared cougars killed by hunters or vehicles) and numbers of cougar mortalities recorded by year near Cle Elum, WA, 2002–2007

	2002	2003	2004	2005	2006	2007
Collared	14	19	20	16	16	16
Collared mortalities	1	1	5	1	1	9
Uncollared mortalities	5	2	4	3	1	4

**Table 2** Mortality rates (mean  $\pm$  sd) and sample sizes (number of dead animals in parentheses) of radio-collared cougars *Puma concolor* near Cle Elum, WA, 2002–2007

Sex and age class	Mortality source			
	<i>n</i>	Hunting	Vehicle	Natural
Female				
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)
Male				
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)

sd, standard deviation.

**Table 3** 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 *Puma concolor* near Cle Elum, WA, 2002–2007

Age class	Females			Males		
	Radio days	<i>n</i>	Survival rate	Radio days	<i>n</i>	Survival rate
Kitten (0–12 months)	1094	1 (6)	0.7162 $\pm$ 0.24	2295	4 (13)	0.5290 $\pm$ 0.17
Juvenile (13–24 months)	1310	1 (5)	0.7567 $\pm$ 0.21	1084	2 (8)	0.5095 $\pm$ 0.24
Adult (25+ months)	7601	3 (12)	0.8658 $\pm$ 0.07	5851	7 (12)	0.6461 $\pm$ 0.11
Total (all ages)	10 005	5 (23)	0.8332 $\pm$ 0.07	9230	13 (33)	0.5978 $\pm$ 0.08

sd, standard deviation.

## Population density

Density calculations using the total number of whole animals within the mean annual 95% composite female range (655 km<sup>2</sup>, 95% CI = 425–885) yielded a mean density of 4.97 animals/100 km<sup>2</sup>. Adult male density was 1.50/100 km<sup>2</sup> and adult female density was 1.15/100 km<sup>2</sup>. Our second method calculated density using the proportion of time animals spent inside the mean annual 95% composite female range. The mean density of total animals was 3.33 animals/100 km<sup>2</sup>, adult males was 0.64 animals/100 km<sup>2</sup> and adult females was 1.09 animals/100 km<sup>2</sup>. Total density did not change significantly over the study period for either method (Method 1:  $F = 1.37$ ,  $P = 0.31$ , for all regressions: MS regression d.f. = 1, MS residual d.f. = 4; Method 2:  $F = 0.98$ ,  $P = 0.38$ ; Fig. 2). Adult female density did not significantly change (Method 1:  $F = 0.10$ ,  $P = 0.77$ ; Method 2:  $F = 0.11$ ,  $P = 0.76$ ), while adult male density declined using both methods (Method 1:  $F = 6.61$ ,  $P = 0.06$ ; Method 2:  $F = 6.75$ ,  $P = 0.06$ ).

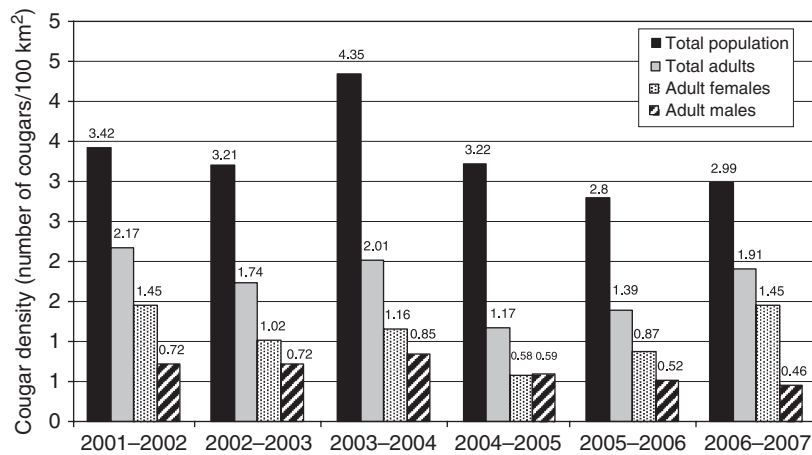
## Age structure

Mean age of the population was 41 months (3.4 years), mean age of adult males was 60 months (5 years), and mean age of adult females was 69 months (5.8 years). 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 as predicted by the closed population hypothesis. 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 net emigration of radio-collared cougars. Our findings reject the closed population hypothesis and support the open population hypothesis for typically sized game management units. 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.

We may have missed some cougars that were present on the landscape during the study. However, our population estimates of collared and uncollared cats were derived by back-dating each animal's lifespan to date of birth (females) or date of immigration (males) throughout the time series. This method would reduce 'missed cats' for any given preceding year because the trapping effort is 'cumulative' over time. Furthermore, missing or adding the same average number of cougars each year would not change the observed



**Figure 2** Total and adult cougar *Puma concolor* (> 24 months old) densities (cougars/100 km<sup>2</sup>) within the Cle Elum study area in central Washington, August 2001 to August 2007. Densities were calculated using the proportion of male and female locations that fell inside the mean annual 95% composite female home range.

growth and emigration rates – but simply increase density estimates. A temporal bias such as missing cougars only early in the study (most likely error because of relative trapping inexperience in the area) would yield an even lower true observed growth rate while missing cougars only later in the study (least likely error because of relative trapping experience in the area) 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 we missed three cougars in 2002, the true growth rate would have been 11/13, or 0.85. We have neither reason nor evidence to suspect that we missed more cougars as the study progressed.

The 22 animals that went undetected by our ground tracking efforts, but that were ‘detected’ by hunters and a vehicle collision within the study area may have resulted from newly transient animals being shot before our winter trapping efforts, or uncollared animals having home ranges that were largely located outside of the 655 km<sup>2</sup> study area. The open nature, or lack of confining landscape features, allowed collared cougar movements to cross study area boundaries freely. On average, only 43% of male GPS locations fell inside the study area boundary (Fig. 1).

The 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, Irwin & Skinner, 1986; Logan & Sweanor, 2001; Anderson & 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 years) in the hunted area and 55.2 months (4.6 years) in the unhunted area]. Robinson *et al.* (2008) also reported significantly ( $P < 0.05$ ) lower mean ages of adult females (46 months, 3.8 years) and adult males (41 months, 3.4 years) in a heavily hunted population, compared with a mean age of 69 months (5.8 years) for adult females and 60 months (5 years) for adult males in this study. The relatively low hunting mortality ( $0.11 \pm 0.04$ )

in this study compared with  $0.24 \pm 0.07$  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 and associated territorial nature of resident animals in this population may limit immigration and enhance emigration of younger male animals. Logan & Sweanor (2001) found that adult males often exhibit territorial behavior, including repulsion of males through fighting, and exclusiveness of home ranges. The net emigration response of male progeny, along with recruitment of female progeny, and a positive stochastic growth rate, indicates that this population may be self-sustaining and may serve as a population source to the region (Thomas & Kunin, 1999; Sweanor *et al.*, 2000). 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).

## Implications for conservation and management

Our findings suggest that emigration counters high survival/fecundity population growth in this lightly hunted area. 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. These metapopulation interactions appear to act as a stabilizing force to sub-populations (Pulliam, 1988; Sweanor *et al.*, 2000) in both the absence and presence of high hunting mortality, at least at the smaller game management unit scales (<1000 km<sup>2</sup>) observed in these studies, and where prey density is adequate (Pierce, Bleich & Bowyer, 2000). Heavy hunting (mortality rate = 0.38) at a large scale (30 000 km<sup>2</sup>) 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.*, 2006; Robinson *et al.*, 2008).

Heavy hunting in typical 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 in such units do not correspond with increased cougar numbers and densities as commonly believed. Immigration and emigration countered the population declines and increases predicted by the closed population hypothesis. These findings have two management implications: (1) cougar populations interact at landscape scales through immigration and emigration (metapopulations), so management at small scales may be inappropriate (Sweaner *et al.*, 2000; Stoner *et al.*, 2006; Robinson *et al.*, 2008) and (2) 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 at the game management unit scale.

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