

Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis

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Abstract. Many wildlife species are managed based on the compensatory mortality hypothesis, which predicts that harvest mortality (especially adult male mortality) will trigger density-dependent responses in reproduction, survival, and population growth caused via reduced competition for resources. We tested the compensatory mortality hypothesis on two cougar (*Puma concolor*) populations in Washington, USA (one heavily hunted and one lightly hunted). We estimated population growth, density, survival, and reproduction to determine the effects of hunting on cougar population demography based on data collected from 2002 to 2007. In the heavily hunted population, the total hunting mortality rate (mean \pm SD) was 0.24 ± 0.05 (0.35 ± 0.08 for males, 0.16 ± 0.05 for females). In the lightly hunted population, the total hunting mortality rate was 0.11 ± 0.04 (0.16 ± 0.06 for males, 0.07 ± 0.05 for females). The compensatory mortality hypothesis predicts that higher mortality will result in higher maternity, kitten survival, reproductive success, and lower natural mortality. We found no differences in rates of maternity or natural mortality between study areas, and kitten survival was lower in the heavily hunted population. We rejected the compensatory mortality hypothesis because vital rates did not compensate for hunting mortality. Heavy harvest corresponded with increased immigration, reduced kitten survival, reduced female population growth, and a younger overall age structure. Light harvest corresponded with increased emigration, higher kitten survival, increased female population growth, and an older overall age structure. Managers should not assume the existence of compensatory mortality when developing harvest prescriptions for cougars.

Key words: carnivore; compensatory mortality hypothesis; cougar; density; emigration; hunting; immigration; mortality; population growth; *Puma concolor*; source-sink; survival.

INTRODUCTION

Density-dependent population regulation has been experimentally demonstrated for a variety of animals and forms the theoretical basis for sustainable hunting of polygynous mammals (Caughley 1977, Caughley and Sinclair 1994, Ginsberg and Milner-Gulland 1994, Strickland et al. 1994). The compensatory mortality hypothesis predicts that harvest mortality, especially of adult males, triggers density-dependent responses in reproduction, offspring survival, and female population growth by reducing competition for resources (Connell 1978). In unhunted or lightly harvested populations, higher densities generate increased competition for resources, resulting in decreased reproduction, offspring survival, and female population growth. Therefore, removal of adult males in polygynous mating systems

is generally considered to have benign or beneficial effects on population growth (Errington 1945, Frank and Woodroffe 2001, Johnson et al. 2001).

The compensatory mortality model has been demonstrated for a variety of ungulates (Staines 1978, Burnham and Anderson 1984, Peek 1986, Bartmann et al. 1992, White and Bartmann 1998), but little evidence suggests that the model fits carnivore populations (Franke and Woodroffe 2001, Milner et al. 2007). Because life histories of carnivores and ungulates differ, we would also expect that density dependence might operate differently. Ungulates typically have restrictive or limited dispersal movements compared to carnivores (Chepko-Sade and Halpin 1987, Howe et al. 1991, Franke and Woodroffe 2001, Zimmerman et al. 2005, Whitman et al. 2007). Therefore hunting males is likely to reduce local herbivore densities but may not have the same effect on carnivores, which display long-distance, density-independent dispersal by males. Such intrinsic emigration can depress population density, and intrinsic immigration can increase population density regardless of birth and death rates (Franke and Woodroffe 2001, Festa-Bianchet 2003). This exchange of animals via immigration and emigration may offset expected chang-

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es in density and associated effects on vital rates of resident female animals. As a result, harvest levels that are considered beneficial or benign to an ungulate population may impose additive mortality on carnivores (Franke and Woodroffe 2001, Festa-Bianchet 2003, Swenson 2003).

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

We tested whether hunting supported the compensatory mortality hypothesis by comparing demographic parameters from two Washington State cougar populations, one heavily hunted and one lightly hunted, from 2002 to 2007. The compensatory mortality hypothesis predicts that heavy hunting of cougars will result in (1) decreased male densities, (2) increased maternity rates, (3) increased survival of young, (4) decreased natural mortality, and (5) increased female population growth; and that low levels of harvest will result in (1) increased male densities, (2) decreased maternity rates, (3) decreased survival of young, (4) higher natural mortality rates, and (5) decreased female population growth.

STUDY AREAS

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

Heavily hunted area (HH)

The 735-km² study area lies north of the town of Kettle Falls, and includes a patchwork of federal, state, and privately owned lands. The study area is bounded on the southeast and southwest by the Columbia and

Kettle Rivers. The Canadian–United States border forms the northern boundary. The area is part of a glacially subdued mountainous region (400–2130 m elevation) known as the Okanogan Highlands, and occupies the transition between the East-slope Cascades and Northern Rocky Mountain physiographic province (Bailey et al. 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the 46-cm annual precipitation falls as snow, with an average of 136 cm falling from mid-November to mid-April annually. Mean annual temperatures range from –6°C in January to 21°C in July. White-tailed deer (*Odocoileus virginianus*) are the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) are also present. Common predator species besides cougar include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*).

Lightly hunted area (LH)

The study area is located along the East-slope foothills of the North Cascades Mountains near the town of Cle Elum. The area covers 594 km² and includes a portion of the upper Yakima River watershed. The study area is bounded by the Cascade Mountains on the west, the Enchantment Wilderness on the north, and unforested agricultural lands of the Kittitas Valley on the south and east. Sagebrush steppe foothills (below 550 m elevation) transition upward to slopes covered with ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) dominate ridges at elevations >1550 m. Precipitation averages 56.4 cm/yr, with 160 cm of snowfall during winter. Mean annual temperature ranges from –7°C in January to 27°C in July. Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species besides cougar include coyotes, black bears, and bobcats.

METHODS

Captures and monitoring

We attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of each study area during winter when tracks can be detected in snow. We used hounds to track and tree cougars (Hornocker 1970). We immobilized treed cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 mL/10 kg of body mass, or with Telazol at a dosage of 6 mg/kg, using a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). We determined sex and classified animals as kittens (0–12

months), juveniles (13–24 months), or adults (25+ months) based on physical measurements and gum regression measurements of the canine teeth (Laundre et al. 2000).

We fitted each animal with a mortality-sensing Very High Frequency collar (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA) or Global Positioning System (GPS; Lotek Wireless, Newmarket, Ontario, Canada and Televilt, Lindesberg, Sweden). Beginning in January 2005, we investigated den sites of collared females and captured kittens by hand. We implanted kittens <6 weeks old with PIT (Passive Integrated Transponder) tags (AVID, Norco, California, USA), and collared kittens that were >6 weeks old with expandable VHF (Telonics, Mesa, Arizona, USA; T. Ruth, *personal communication*) radio collars to accommodate growth. We handled all animals in accordance with Washington State University Animal Care (IACUC Permit #3133) and Animal Welfare Assurance Committee (AWAC Permit #A3485-01). GPS collars were programmed to collect locations at 4-hour intervals (six times/day). The data were retrieved using a remote communication unit. We recorded location coordinates of VHF-collared animals at one-week intervals from ground or aerial telemetry.

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

We used the modified Mayfield method (Heisey and Fuller 1985) to estimate survival of animals because it provides increased precision when mortality rates are high, performs well in the case of small sample size typical of large carnivore species, and can identify cause-specific mortality rates (Winterstein et al. 2001, Murray 2006). We calculated annual survival rates for male and female kittens, juveniles, and adults from January 2002 to December 2007.

To determine intervals when survival probabilities were constant, we analyzed the statistical distribution of deaths over a 365-day period (Lambert et al. 2006). This yielded 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 September 31). Annual survival was the product of seasonal survival rates (Heisey and Fuller 1985). We chose intervals for each period 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 a one-tailed z test to determine whether survival rates in LH were higher than in HH (Micromort version 1.3; Heisey and Fuller 1985).

Maternity and fecundity

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

Deterministic and stochastic growth rates

We constructed a survival/fecundity dual-sex Leslie matrix (Leslie 1945) to model closed-population growth for each area using RAMAS GIS (Akçakaya 2002). We assigned female age at first reproduction as 24 months, assumed an equal sex ratio at birth, and maximum age or age at senescence of 13 years (Robinson et al. 2008).

We calculated the deterministic growth rate (λ_D) as the dominant eigenvalue of the matrix under a stable age distribution. We calculated the stochastic growth rate (λ_S) by incorporating annual environmental variability (standard deviation 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 in RAMAS GIS (Akçakaya 2002). We sampled vital rates from a lognormal distribution to avoid truncations, which can occur if standard deviations are large due to sampling and measurement error. We projected each population for six years (five transitions), and calculated λ_S as the average geometric mean growth rate from 200 simulations, the point at which rates converged (Robinson et al. 2008).

Observed growth, immigration, and emigration

We determined observed growth rates (λ_O) from annual counts of collared and unmarked cougars. Each year we tallied the number of cougars (adults, juveniles,

TABLE 1. Sources of mortality of radio-collared cougars in northeast (HH, heavily hunted) and central (LH, lightly hunted) Washington State, 2002–2007.

HH area				
Sex and age	<i>n</i>	Hunting	Depredation	Natural
Female				
Kitten (0–12 months)	10		0.14 ± 0.13 (1)	0.54 ± 0.18 (4)
Juv. (13–24 months)	6			
Adult (24+ months)	19	0.22 ± 0.07 (7)		0.12 ± 0.06 (4)
Total	35	0.16 ± 0.05 (7)	0.02 ± 0.02 (1)	0.18 ± 0.06 (8)
Male				
Kitten (0–12 months)	13			0.69 ± 0.14 (6)
Juv. (13–24 months)	12	0.46 ± 0.17 (4)		
Adult (24+ months)	12	0.46 ± 0.12 (8)	0.06 ± 0.24 (1)	
Total	37	0.35 ± 0.08 (12)	0.03 ± 0.03 (1)	0.17 ± 0.06 (6)
Population totals	72	0.24 ± 0.05 (19)	0.03 ± 0.02 (2)	0.18 ± 0.04 (14)

Note: Sample sizes (*n* = total number of animals at risk), mortality rates (mean ± SD), and number of mortalities (in parentheses) are shown.

and kittens) in each study area and calculated λ_O as $\lambda_x = (n_t/n_0)^{1/t}$, where λ_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 to determine whether deterministic (λ_D) and stochastic (λ_S) growth rates were higher than the average six-year observed (λ_O) growth rate for LH, and whether λ_D and λ_S were lower than λ_O for HH (Zar 1999). We estimated net immigration/emigration rate (i/e) using the equations $i/e = \lambda_D - \lambda_O$ and $e = \lambda_S - \lambda_O$ (Peery et al. 2006). We also used observations of radio-collared cougars to document net emigration and immigration in each area from 2005 through 2007, the period during which we radio-monitored kittens (radio collars enabled us to document emigrants).

Population density

We estimated mean annual densities of cougars (number of cougars/100 km²) for each study area as the number of animals multiplied by the mean proportion of male and female locations that fell inside a mean annual 95% composite kernel home range of collared females (McLellan 1989). For unmarked cougars, we used the mean proportion of marked animals. We back-calculated the life span of each marked and unmarked cougar to the beginning of the study, its birth date (females), or immigration date (males) as described by Logan and Sweanor (2001:66), Stoner et al. (2006), and Robinson et al. (2008). We used a general linear model (GLM) to test for independent effects of study area and time on cougar density. We included study area, time, time², time × study area, and time² × study area as independent variables and then selected variables stepwise in a backward fashion, removing those that failed to be significant at the 0.10 probability level (Zar 1999).

Age structure

We calculated sex ratios (F:M) from collared cougars only to prevent bias that may result from hunters

selecting for male cougars (trophies). We determined whether ratios were different from equality with a chi-square goodness-of-fit test (Zar 1999). We compared mean age of cougars in each area with a two-sample t test and examined the trend over time in age structure with simple linear regression (Zar 1999).

Confounding factors

To account for possible differences in per capita resources affecting maternity, kitten survival, and female population growth, we compared cougar densities and female predation rates in the two study areas. We compared densities with a general linear model and tested for differences in predation rates with a two-tailed t test (Zar 1999).

RESULTS

Captures and monitoring

We captured and marked 103 cougars in the two study sites (57 in HH, 46 in LH) between January 2002 and December 2007. Hunters killed 50 unmarked cougars (nine females, 13 males in HH; 14 females, 13 males, one of unknown sex in LH), and one uncollared female in LH was killed by a vehicle collision. We observed 26 unmarked kittens (six females, two males, nine of unknown sex in HH; three females, four males, two of unknown sex in LH) traveling with collared females.

Survival and mortality

Fifty-three (35 in HH, 18 in LH) radio-collared cougars died during the study (Table 1). Hunters killed 26 cougars, 22 died from natural causes, three died in vehicle collisions, and two were killed from depredation hunts. Eight juveniles (two in HH, six in LH) emigrated and were censored at the last known date of their location. An additional nine (four in HH, five in LH) animals were censored due to shed collars or lost VHF signals. Of 42 radio-collared kittens, 18 survived to one

TABLE 1. Extended.

<i>n</i>	LH area		
	Hunting	Vehicle	Natural
6			0.28 ± 0.24 (1)
5	0.24 ± 0.21 (1)		
12	0.04 ± 0.04 (1)		0.09 ± 0.06 (2)
23	0.07 ± 0.05 (2)		0.10 ± 0.05 (3)
13			0.47 ± 0.17 (4)
8	0.25 ± 0.22 (1)	0.25 ± 0.22 (1)	
12	0.20 ± 0.09 (4)	0.10 ± 0.07 (2)	0.05 ± 0.05 (1)
33	0.16 ± 0.06 (5)	0.09 ± 0.05 (3)	0.16 ± 0.06 (5)
56	0.11 ± 0.04 (7)	0.05 ± 0.03 (3)	0.13 ± 0.04 (8)

year of age, 16 died from natural causes, and four were censored. Six of the “natural” kitten mortalities in HH (three females, two males, one unknown sex) were presumed to have been killed by male cougars, as confirmed by canine tooth punctures in the skull and close proximity of a collared male at estimated time of death.

Average annual survival rates, including all sources of mortality, for all radio-collared cougars in HH were 0.56 ± 0.05 (mean \pm SD) and 0.71 ± 0.06 in LH, but survival varied with age and sex classes (Table 2). Overall survival and survival of adults was higher in LH than in HH (overall: $Z = 1.98$, $P = 0.02$; adults: $Z = 1.75$, $P = 0.04$). Survival of adult females and survival of kittens was also higher in LH (adult females: $Z = 1.88$, $P = 0.03$; kittens: $Z = 1.49$, $P = 0.07$). We did not detect differences among other sex or age comparisons. Overall mortality rate from hunting was higher ($Z = 2.02$, $P = 0.04$) in HH (0.24 ± 0.05) than in LH (0.11 ± 0.04). We found no differences in natural mortality rates (HH = 0.18 ± 0.04 , LH = 0.13 ± 0.04 ; $Z = 0.77$, $P = 0.44$). The standard deviation of annual survival rates, including all sources of mortality for all cougars, was 0.09 in HH and

0.06 in LH. These values were used in the standard deviation matrix of RAMAS. We removed the six kittens from the analysis that were killed by male cougars in HH, recalculated survival rates, and found that kitten survival was not different ($Z = 0.96$, $P = 0.96$) in HH (0.59 ± 0.02) and LH (0.58 ± 0.02).

Maternity and fecundity

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

Population growth

The deterministic annual female growth rate (λ_D) based on survival and fecundity models was 0.80 in HH and 1.13 in LH. The stochastic growth rate (mean $\lambda_S \pm$ SD) for HH (0.78 ± 0.19) was lower than in LH (1.10 ± 0.12 ; $t = 21.09$, $P < 0.01$). The observed growth rates (λ_O) based on the actual number of cougars in the study area were 0.91 (female $\lambda_O = 0.86$, male $\lambda_O = 1.02$) for HH and 0.98 (female $\lambda_O = 0.97$, male $\lambda_O = 0.96$) for LH, and were not different ($t = 0.86$, $P = 0.42$). Modeled growth rates were significantly higher than λ_O in LH (for λ_D , $t = 2.09$, $P = 0.05$; for λ_S , $t = 1.68$, $P = 0.09$) and lower than λ_O in HH (for λ_D , $t = 2.10$, $P = 0.07$; for λ_S , $t = 2.46$, $P = 0.05$). The HH population had net immigration rates of 0.11 ($\lambda_O - \lambda_D$) and 0.13 ($\lambda_O - \lambda_S$), and the LH population had net emigration rates of 0.12 ($\lambda_O - \lambda_S$)

TABLE 2. Radio-days and survival rates (mean \pm SD) by sex and age class for radio-collared cougars in northeast (HH, heavily hunted) and central (LH, lightly hunted) Washington State, 2002–2007.

Sex and age	HH area			LH area		
	Radio-days	<i>n</i>	Survival rate	Radio-days	<i>n</i>	Survival rate
Female						
Kitten (0–12 months)	1611	5 (10)	0.32 ± 0.16	1094	1 (6)	0.72 ± 0.24
Juvenile (13–24 months)	1871	0 (6)	1.00 ± 0.00	1310	1 (5)	0.76 ± 0.21
Adult (24+ months)	9645	11 (19)	0.66 ± 0.08	7601	3 (12)	0.87 ± 0.07
Total	13 126	16 (35)	0.64 ± 0.07	10,005	5 (23)	0.83 ± 0.07
Male						
Kitten (0–12 months)	1885	6 (13)	0.31 ± 0.15	2295	4 (13)	0.53 ± 0.17
Juvenile (13–24 months)	2392	4 (12)	0.54 ± 0.52	1084	2 (8)	0.51 ± 0.24
Adult (24+ months)	4470	9 (12)	0.48 ± 0.12	5851	7 (12)	0.65 ± 0.11
Total	8746	19 (37)	0.45 ± 0.08	9230	13 (33)	0.60 ± 0.08
Population totals	21 872	35 (72)	0.56 ± 0.05	19,235	18 (56)	0.71 ± 0.06

Note: Sample size *n* is the number of mortalities, with the total number of monitored animals in parentheses.

TABLE 3. Densities and ages (mean \pm SD) for monitored cougars in northeast (HH, heavily hunted) and central (LH, lightly hunted) Washington State, 2002–2007.

Age and sex	HH area		LH area	
	Density (cougars/100 km ²)	Age (months)	Density (cougars/100 km ²)	Age (months)
Adults (>24 months)				
Female	1.35 \pm 0.12	51 \pm 7	1.07 \pm 0.38	68 \pm 13
Male	0.23 \pm 0.10	42 \pm 5	0.80 \pm 0.05	59 \pm 5
Total	1.58 \pm 0.17	48 \pm 5	1.87 \pm 0.42	61 \pm 3
All ages				
Female	2.83 \pm 0.76	33 \pm 7	2.32 \pm 0.44	40 \pm 6
Male	0.63 \pm 0.12	24 \pm 5	1.30 \pm 0.15	41 \pm 5
Total	3.46 \pm 0.69	27 \pm 4	3.62 \pm 0.58	39 \pm 4

and 0.15 ($\lambda_O - \lambda_D$). Observations of radio-collared cougars supported these trends; we documented five emigrants and three immigrants in LH, and four immigrants and zero emigrants in HH from 2005 through 2007.

Population density

The mean 95% composite range of females was 772 km² (95% CI = 316–1228) for HH and 655 km² (95% CI = 425–885) for LH. The annual proportion (mean \pm SD) of male GPS points within the composite range of females was 0.32 \pm 0.08 in HH and 0.43 \pm 0.16 in LH.

Time and time \times area explained significant variation in cougar density ($P < 0.10$). The final model included: area, time, and time \times area. Mean annual densities of all cougars were 3.46 \pm 0.69/100 km² in HH and 3.62 \pm 0.58/100 km² in LH, and were not different ($P = 0.26$) (Tables 3 and 4). Compared to LH, mean densities of males were lower in HH (0.63 \pm 0.12 vs. 1.30 \pm 0.15/100 km²; $P < 0.01$) and mean densities of females were higher (2.83 \pm 0.76 vs. 2.32 \pm 0.44; $P = 0.02$). Within HH, densities of all cougars and females declined over the study period, whereas we detected no change in male densities. In LH, we did not detect a change in density for any sex and age class (all $P > 0.05$; Table 4).

Sex and age structure

Mean age of the cougar population was 27 months (2.3 years) in HH and 38 months (3.2 years) in LH (Table 3). Most mean ages of cougars were higher in the LH than in HH for all age and sex classes (all $P < 0.05$), with one exception being mean age of females, which was actually higher in the HH ($P = 0.10$) (Table 3). Mean age of female cougars in HH increased ($P = 0.03$) over time and mean age of males decreased ($P = 0.07$). We detected no changes in age for LH ($P > 0.10$) across the study period.

Confounding factors

We detected no differences in mean maternity rates ($t = 2.26$, df = 9, $P = 0.94$), predation rates ($t = 0.79$, df = 34, $P = 0.44$), or population density ($t = 1.47$, df = 1, $P = 0.26$) between areas. The female predation rate in HH

was 6.68 days/kill (Cooley et al. 2008) and 7.04 days/kill in LH (K. White, *unpublished data*).

DISCUSSION

Data comparing demographics of two Washington cougar populations suggest that hunting does not act in a compensatory manner in cougar populations. The compensatory mortality hypothesis predicts that increased harvest mortality of males will reduce population density, resulting in lower competition for resources, reduced natural mortality, and increased reproduction and survival of young. The compensatory mortality hypothesis predicted that low levels of harvest will result in increased densities and rates of natural mortality, and decreased reproduction and survival.

In the heavily hunted area, female densities declined and male densities remained unchanged, whereas we

TABLE 4. Effects of study area (hunting level) and time (2002–2007) on density estimates of cougars (cougars/100 km²) using a general linear model.

Parameter	Estimate	SE	<i>t</i>	<i>P</i>
Total cougars				
Intercept	4.05	0.38	10.71	<0.01
HH area	0.65	0.54	1.21	0.26
LH area	0.00			
Time	−0.15	0.10	−1.53	0.17
Time \times area HH	−0.27	0.14	−1.94	0.09
Time \times area LH	0.00			
Male cougars				
Intercept	1.41	0.14	10.17	<0.01
HH area	−0.78	0.20	−3.97	<0.01
LH area	0.00			
Time	−0.04	0.04	−1.04	0.33
Time \times area HH	0.02	0.05	0.47	0.65
Time \times area LH	0.00			
Female cougars				
Intercept	2.64	0.33	7.92	<0.01
HH area	1.43	0.47	3.02	0.02
LH area	0.00			
Time	−0.11	0.09	−1.30	0.23
Time \times area HH	−0.29	0.12	−2.38	0.04
Time \times area LH	0.00			

observed no change in male or female densities in the lightly hunted area. We found no differences in rates of natural mortality (0.18 in the heavily hunted area and 0.13 in lightly hunted area) or maternity rates (1.15 in the heavily hunted area vs. 1.12 in lightly hunted area). Kitten survival was lower in the heavily hunted area (0.32 in the heavily hunted area and 0.58 in the lightly hunted area), with none of the kitten mortalities resulting from hunting or death of the mother. Our findings reject the compensatory mortality hypothesis because vital rates did not compensate for hunting mortality.

Resource availability could have influenced vital rates; however, both populations were at similar densities (3.46 cougars/100 km² in the heavily hunted area and 3.62 cougars/100 km² in the lightly hunted area) and female predation rates were not different, suggesting that resources were similar between areas. Densities were maintained via a net immigration into the heavily hunted area and a net emigration out of the lightly hunted area. The net emigration could indicate poorer resources; however, kitten survival and female population growth were higher there, suggesting that this is not the case. The net immigration rate in the heavily hunted area could suggest better resources, but kitten survival and female population growth were lower there, also contrary to the compensatory mortality hypothesis.

Instead of hunting influencing survival and reproduction, hunting was compensated by immigration and emigration in both cougar populations. The stochastic population model, based on the compensatory mortality hypothesis, predicted a 27% population decline, whereas we observed a 9% decline in overall numbers and no decline in the male population. The difference in growth rates resulted from immigration. The stochastic model assumed a closed population structure and did not account for immigration, whereas the observed growth rate accounted for the open nature of cougar populations by including immigration. Many of the mortalities resulting from hunting were replaced by animals immigrating from surrounding areas.

In the lightly hunted population, the stochastic model predicted a 10% increase in population growth, yet cougar numbers remained stable. The projected population increase was compensated by emigration rather than by decreased vital rates. Therefore, neither total population density nor competition among cougars appeared to be influenced by hunting, with immigration and emigration counteracting the effects predicted by the compensatory mortality hypothesis.

Long-distance dispersal is common in cougars (Sweanor et al. 2000, Logan and Sweanor 2001, Stoner et al. 2006) and can help to maintain overall numbers by replacing harvest mortalities with animals dispersing from neighboring areas (Hanski 2001). Rebound from heavy hunter harvest by immigration has been documented in cougar populations elsewhere (Ross and Jalkotzy 1992, Logan et al. 1986, Logan and Sweanor

2001, Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008). As a consequence, harvest models based on compensatory mortality hypothesis are unable to accurately predict the responses of cougar populations to hunting.

The heavily hunted population compensated for heavy harvest in overall numbers of cougars through male immigration. However, the female population declined ($\lambda_O = 0.86$). Although male cougars commonly disperse long distances, females are usually philopatric (Sweanor et al. 2000). As a result, fewer female immigrants are available to immigrate and replace those that are harvested, resulting in decreased numbers of females. Adult female survival is therefore vital for population growth and recovery from harvest (Martorello and Beausoleil 2003).

Harvesting adult males may increase incidences of infanticide by allowing immigration of new, unrelated males (Ross and Jalkotzy 1992, Whitman and Packer 1997, Murphy et al. 1999, Logan and Sweanor 2001). Lower kitten survival in the heavily hunted area may be a result of high male turnover from hunting. Male carnivores are known to kill unrelated young in order to induce estrous and gain breeding opportunities (Packer and Pusey 1983, Smith and McDougal 1991, Wielgus and Bunnell 1995, Swenson et al. 1997, Logan and Sweanor 2001). Our observations suggest that six kittens of three litters in the heavily hunted area may have been killed by unrelated male cougars. When we removed those six kittens from the survival analysis, we found no difference in survival rates of kittens between areas, suggesting that infanticide may have been responsible for lower kitten survival in the heavily hunted area. High rates of immigration following heavy male harvest were also documented for brown bears *Ursus arctos* (Wielgus and Bunnell 1994) and black bears *Ursus americanus* (Sargeant and Ruff 2001). Female population growth declined because of sexually selected infanticide in brown bears (Wielgus and Bunnell 1994, Swenson et al. 1997). This may indicate that the compensatory mortality hypothesis may not be appropriate for many solitary, territorial, or quasi-territorial carnivores.

It is unlikely that age structure ever stabilizes in long-lived species such as cougars, which may bias our estimates of deterministic growth. Because this lack of variability assumes a stable age distribution, we have little confidence that differences between deterministic growth rates and observed growth rates act as predictors of actual population growth and believe that differences between stochastic growth rates and observed growth rates more accurately project growth rates. Additionally, despite intense trapping efforts conducted each winter, we may have missed some cougars that were present on the landscape during the study, resulting in biased estimates of observed growth and subsequent net immigration and emigration rates. The addition of the same number of cougars each year would increase density estimates, but would not change the observed

growth and emigration rates. A temporal bias, such as missing cougars only early in the study (most likely error), would yield an even lower true observed growth rate, whereas missing cougars only later in the study (least likely error) would yield a higher true observed growth rate. For example, a count of 10 cougars in 2002 and 11 cougars in 2003 would yield an observed growth rate of 1.10. If 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, therefore any bias in our observed population growth rates is conservative.

CONSERVATION IMPLICATIONS

Harvest models that are based on the compensatory mortality hypothesis rely on the assumption that density reductions result in reduced competition for resources, thereby increasing survival and reproduction of remaining animals. However, our results suggest that dispersal movements may mitigate for mortalities resulting from hunting and negate compensation by other vital rates. These findings have two management implications. (1) Recovery from harvest relies on nearby source populations; therefore, cougar harvest should be managed at the metapopulation scale (Cougar Management Guidelines Working Group 2005:73–74). (2) Even when healthy source populations exist, prolonged harvest will cause female population declines via direct harvest of adult males and increased kitten mortality caused by immigration of potentially infanticidal males (Ross and Jalkotzy 1992, Logan and Sweanor 2001), and kitten abandonment from harvest of mothers (R. Beausoleil, *personal communication*). The compensatory mortality hypothesis may not be appropriate for modeling hunter harvest for cougars and other large carnivores that exhibit long-distance dispersal. Assumptions of closed populations are not appropriate for solitary carnivore species.

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APPENDIX

Comparison of seasonal survival by year for radio-collared cougars in central (LH, lightly hunted) and northeast (HH, heavily hunted) Washington State, USA, 2002–2007 (*Ecological Archives* E090-207-A1).