



Effects of male trophy hunting on female carnivore population growth and persistence



Robert B. Wielgus^{a,*}, Dana Eleanor Morrison^a, Hilary S. Cooley^b, Ben Maletzke^c

^a Large Carnivore Conservation Laboratory, School of Environment, Washington State University, Pullman, WA 99164-6410, USA

^b U.S. Fish and Wildlife Service, Boise, ID, USA

^c Washington Department of Fish and Wildlife, Olympia, WA 98501, USA

ARTICLE INFO

Article history:

Received 17 May 2013

Received in revised form 3 July 2013

Accepted 8 July 2013

Keywords:

Hunting

Cougars

Population growth

Compensatory mortality

Additive mortality

Depensatory mortality

ABSTRACT

Carnivore populations are often 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. Our previous research on grizzly bears (*Ursus arctos*) and cougars (*Puma concolor*) 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 male carnivores has a negative additive or depensatory effect on female population growth depending on the intensity of male mortality. We recommend that hunting of polygynous carnivores not exceed their intrinsic growth rates to forestall excessive compensatory male immigration and infanticide. The Washington Department of Fish and Wildlife instituted a new “equilibrium” hunting management plan (hunting mortality < 14%/year) for cougars in 2013 based on our findings and recommendations.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

There are three 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., 2006](#)). (2) Natural mortalities and reproduction remain unchanged regardless of hunting (density independent, additive mortality model: [Allen et al., 2006](#)). (3) Natural mortalities increase and reproduction declines (inversely density dependent, depensatory mortality model: [Wielgus and Bunnell, 1994a,b, 2000](#); [Sinclair](#)

[et al., 2006](#)). All three responses have been observed in wildlife populations. For example: [Anderson and Burnham \(1976\)](#) 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. [Wielgus and Bunnell \(1994a,b\)](#) and [Swenson et al. \(1997\)](#) found depensatory effects for reproduction and cub survival in brown bears (*Ursus arctos*).

Sport or trophy hunting of male 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

* Corresponding author. Tel.: +1 509 335 2796, mobile: +1 509 595 1232; fax: +1 509 335 7862.

E-mail address: wielgus@wsu.edu (R.B. Wielgus).

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 predator interactions; while still maintaining a viable female population (Ross and Jalkotzy, 1992; Logan and Sweeney, 2001; Caro et al., 2009; Treves, 2009). Wielgus and Bunnell (1995, 2000), Wielgus et al. (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*) corresponds with increased male turnover (compensatory immigration), increased sexually selected infanticide, and reduced female population growth rate. These same compensatory dynamics were later suggested for cougars (Logan and Sweeney, 2001; Robinson et al., 2008; Cooley et al., 2009a), tigers (*Panthera tigris*) (Smith and McDougal, 1991), lions (Pusey and Packer, 1994; Packer et al., 2009, 2010) and leopards, (Caro et al., 2009; Packer et al., 2010).

Cooley et al. (2009a) compared a lightly and heavily hunted cougar population while controlling for potential confounding factors such as per capita kill rates of prey and cougar density (per capita food was similar and food was not limiting for either population). 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 compensatory (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 = $0.35 + 0.08$ SD) and a lightly hunted, LH, (hunting mortality rate of males = $0.16 + 0.06$ SD) cougar population where the hunting mortality rates were statistically different at $Z = 2.02$, $P = 0.04$ (Cooley et al., 2009b). The adult male hunting rates were $0.46 + 0.12$ SD in the HH and $0.20 + 0.09$ SD in the LH. We removed the effects of hunting (censored female hunting deaths and plausible infanticides) and recalculated 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., (2009b) 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 (non-hunting) 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 sport hunting in both

areas (male harvest rate = 16–35%, female harvest rate = 10–16%, Cooley et al., 2009b). Females that were obviously accompanied by kittens (spotted kittens < 1 year old) are protected from hunting in Washington, but females without kittens were not. Cougar hunting was permitted in both study areas each year from 01 August/September to 15/31 March.

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 total density (includes all age classes including kittens, juveniles, adults, Cooley et al., 2009a) of 3.62 cougars/100 km², 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 total density of 3.46 cougars/100 km² (Cooley et al., 2009), and a kill rate of 6.68 days between ungulate kills (Cooley et al., 2008). No differences in cougar or prey densities that could bias survival or population growth were observed (Cooley et al., 2009b).

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 km². 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. Land ownership is a mixture of federal, state, and private lands. Predominate vegetation below 550 m is sagebrush steppe, transitioning upward to ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Psuedotsuga 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 North-east Washington State and includes a mix of federal, state, and privately owned land and covers 735 km². 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 (*P. mensiesii*), western hemlock (*T. heterophylla*), ponderosa pine (*P. ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*A. 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 and Jalkotzy, 1992; Spreadbury 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-h intervals. Data were retrieved using a remote communication unit. Location coordinates of VHF-collared animals were recorded at 1-week intervals from ground of 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 (<1 km) of collared males at or near the estimated time of death. There were three cases (3 different litters) of plausible infanticide. In one case, 2 kittens were known to have died of predation within 1–2 days in close proximity (<1 km) to a collared male. In the other 2 cases, 4 kittens from 2 litters had obvious evidence of being preyed upon (tooth puncture marks etc.) by cougars.

The modified Mayfield method (Heisey and 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. Annual 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 and 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 and Fuller, 1985).

To calculate how survival and population growth changed with hunting, female hunting deaths and plausible kitten infanticides were removed from our 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 were entered into RAMAS GIS (Akcakaya, 2002) to estimate population growth. The 1st 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 2nd 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 3rd model removed all effects of hunting, including both female hunting mortalities and plausible kitten infanticides, and is equivalent to a non-hunted control population. The 4th 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 (for females only) 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 (Akcakaya, 2002). We used a closed female population model because we observed no female immigration/emigration (unlike males), and the open-population, observed female population growth rates were the same as the closed-population, survival/fecundity female growth rates in our 3 WA study areas (Lambert et al., 2006; Cooley et al., 2009b).

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 were observed to no longer reproduce, and few cougars survived 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 (GMU 105 Kelly Hill, GMU 336 Taneum, and GMU 335 Teanaway). The deterministic growth rates were calculated by RAMAS GIS for each of the 4 models (hunted, female hunting deaths removed, female hunting deaths and infanticide removed, infanticide removed).

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. unhunted) 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 stage-specific survival or fecundity on population growth (Sinclair et al., 2006), thus determining which life stages are most important for population growth. Elasticities sum to 1.00 and can be interpreted similarly to R^2 values – with larger values being more important for population growth than smaller values. 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 19 adult females, 18 juveniles, and 23 kittens in the HH and 12 adult females, 13 juveniles, and 19 kittens in the LH from January 2002 to December 2007. In the HH; 7 of 19 adults died from hunting and 4 others died from natural causes. Four of 18 juveniles died from hunting and 1 from natural causes. Ten of 23 kittens died from natural causes. Six of the 10 natural kitten deaths were from infanticide. These 6 infanticides occurred among 3 different litters. In the LH; 1 of 12 adults died from hunting and another 2 died of natural causes. Two of 13 juveniles died from hunting and another died from natural causes. Five of 19 kittens died from natural causes – none from infanticide during the study period. No kittens were observed to die from orphanage (loss of mother) in either study area during the study period. The associated age and cause-specific mortality rates are given in Table 1.

With hunting and infanticide included, adult females had a significantly higher survival rate ($Z = 7.143$, $P < 0.01$) 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, $Z = 8.26$, $P < 0.01$), 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 from both study areas, 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 marginally significant difference in survival of juveniles ($Z = 2.0$, $P = 0.05$).

In the HH there was a significant increase in survival for adult females (0.88 vs. 0.66, $Z = 3.4$, $P < 0.01$), juveniles (0.93 vs. 0.62, $Z = 5.4$, $P < 0.01$), and kittens (0.59 vs. 0.31, $Z = 4.2$, $P < 0.01$) after removing hunting mortalities and plausible infanticides. In the LH only juveniles showed a significant increase in survival (0.85 vs. 0.62, $Z = 2.4$, $P = 0.01$) after hunting was removed.

4.2. 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 (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 1st model with hunting deaths and infanticide were 0.38 in HH and 0.46 in LH. There were no significant differences between the HH and LH in any of these reproductive parameters (Cooley et al., 2009b). After removing effects of hunting the fecundity rates were exactly 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 female closed population 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 ± 0.11 in HH and 1.05 ± 0.01 in LH. The difference in stochastic growth rates between areas ($1.05 - 0.78 = 0.27$) was significant at ($t = 12.27$, $P < 0.01$). For Model 2 (excluding hunting 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 ± 0.04 in HH and 1.14 ± 0.03 in LH. The difference ($1.14 - 0.98 = 0.16$) was significantly different at $t = 22.2$, $P < 0.01$. For Model 3 (excluding both 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 ± 0.01 in HH and 1.14 ± 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 (excluding infanticide but including hunting deaths of females) the deterministic growth rate was 0.89 in the HH and baseline 1.05 in the LH. The stochastic growth rates were 0.89 ± 0.17 in the HH and baseline 1.05 ± 0.01 in the LH. There was a significant difference for Model 4 between areas $1.05 - 0.89 = 0.16$, $t = 4.69$, $P < 0.01$). In both populations, the

Table 1

Average annual mortality rates of radio-collared female cougars in the heavily hunted (HH) and the lightly (LH) hunted study areas of Washington from 2002 to 2007.

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

Note: Sample sizes (*n* = total number of animals at risk), mortality rates (mean \pm SD).

^a 0–12 months.

^b 13–24 months.

^c 24+ months.

Table 2

Average annual survival rates of female cougars for each of the 4 models in the heavily hunted study area in Washington from 2002 to 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	<i>n</i>	Model 1	Model 2	Model 3	Model 4
Kitten ^a	23	0.31 ± 0.10	0.31 ± 0.10	0.59 ± 0.10	0.59 ± 0.10
Juvenile ^b	18	0.62 ± 0.06	0.93 ± 0.06	0.93 ± 0.06	0.62 ± 0.06
F Adult ^c	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).

^a 0–12 months.

^b 13–24 months.

^c 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 to 2007. Model 1: with hunting included, Model 2: with hunting deaths removed.

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

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

^a 0–12 months.

^b 13–24 months.

^c 24+ months.

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 ($t = 13.04$, $p < 0.01$) 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 ($t = 7.35$, $P < 0.01$) in growth rate due to hunting mortalities (Model 3–Model 4, $1.14 - 0.89 = -0.25$). There was also a significant difference ($t = 19.51$, $P < 0.01$) in growth rate due to plausible infanticide (Model 3–Model 2, $1.14 - 0.98 = -0.16$). Finally, there was a significant difference ($t = 16.29$, $P < 0.01$) 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.

5. Discussion

Our results reject the compensatory mortality hypotheses (which assumes decreased natural mortality and increased reproduction with increased hunting mortality), because fecundity,

Table 4

Elasticity for female cougars for each of the 2 models in the lightly hunted (LH) study area in Washington from 2002 to 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 to 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

kitten survival, juvenile survival, adult female survival, and female population growth rate did not increase with increasing male hunting mortality. The LH (male mortality at 16%) showed evidence of additive mortality because there were some adult female hunting mortalities (4%) and no corresponding decrease in adult female natural mortalities (LH = 12% vs. HH = 9%, Table 1) – with moderate decreases in female population growth (-0.09) due to effects of hunting. The HH (male mortality at 35%) showed both additive (22% adult female mortality) and compensatory effects (HH natural kitten mortality = 69% vs. LH = 42%, Table 1) – with sharp decreases in female population growth (-0.36).

Overall, our results support the compensatory 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 of 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 increased infanticides (compensatory deaths). Although we observed no orphanages (and resulting deaths) of kittens due to hunting deaths of mothers in this study, such indirect effects have been observed to be important elsewhere (Robinson and DeSimone, 2011).

Our most surprising result was the relatively large negative effect of plausible infanticide. We showed that compensatory 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 11 adult age classes combined) 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. Most other studies of large mammals show highest elasticity for adult females – but that is usually the sum of elasticities for all age and stage classes of adult females combined. We compared the “average” elasticity of all adult age classes against the elasticity of kittens – a more equal and fair comparison. Even if there were no additive female hunting deaths, the HH cougar population would still decline (0.98 ± 0.04) because of compensatory 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. 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 over the long-term for an extant species. Accepting increased infanticide as a real phenomenon resulted in intrinsic growth rates of 1.14 in both areas.

Caro et al. (2009) and Packer et al. (2009) predicted and later observed (Packer et al., 2010) that trophy hunting of males corresponds with 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, 2001), Swenson (2003) and Wielgus et al. (2001) observed the same phenomenon in European and North American brown bears. We now corroborate these hypotheses with our experiment on cougars. Male carnivores are known to kill unrelated young to induce estrous in females (Smith and McDougal, 1991; Ross and Jalkotzy, 1992; Pusey and Packer, 1994; Swenson et al., 1997; Logan and Sweanor, 2001; Swenson, 2003; McLellan, 2005). During our study there were 6 plausible infanticides distributed among 3 separate litters 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., 2009a,b).

Originally, Cooley et al. (2009b) 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 increases. 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 primary (obligate) dispersers (Sweanor 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, closed population, female 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.

6. Conclusions

It appears that hunting mortality of males is not compensatory, but actually depensatory for females in large solitary carnivores. Male mortality rates in excess of the intrinsic rate of increase appears to cause female population decline via additive hunting deaths of females and depensatory infanticidal deaths of kittens, as shown in our HH study area. Male hunting mortality rates equal to or less than the intrinsic rate of increase should allow sustainable harvests, as shown in our LH study area. The Washington Department of Fish and Wildlife adopted a new “equilibrium” hunting management plan statewide in 2013 based on our results and recommendations – limiting hunting mortalities to <14%

annually in any given GMU (Beausoleil et al., 2013). Because there is no evidence for compensatory effects and growing evidence for depensatory effects in large solitary carnivores, we suggest that male mortality be restricted to below the intrinsic rate of increase for other species such as African lions, leopards, tigers, jaguars, brown bears, black bears etc. as well.

References

- Akcakaya, H.R. 2002. RAMAS Metapopulations: Viability Analysis for Stage-structured Metapopulations. Version 4.0. Applied Biomathematics, Setaiet, New York, USA.
- Allen, M.S., Miranda, L.S., Brock, R.E., 2006. Implications of compensatory and additive mortality to the management of selected sportfish populations. *Lakes Reservoirs: Res. Manage.* 3, 67–79.
- Anderson, D.R., Burnham, K.P. 1976. Population Ecology of the Mallard. VI. The Effect of Exploitation on Survival/US Fish Wildlife Service Resource, Publication vol. 128, pp. 1–66.
- Bartmann, R.M., White, G.C., Carpenter, L.H., 1992. Compensatory mortality in a Colorado mule deer population. *Wildl. Monogr.* 121, 1–39.
- Beausoleil, R.A., Koehler, G.M., Maletzke, B.T., Kertson, B.N., Wielgus, R.B. 2013. Research to regulation: cougar behavior as a guide to management. *Wildl. Soc. Bull.*, in press.
- Caro, T.M., Young, C.R., Cauldwell, A.E., Brown, D.D.E., 2009. Animal breeding systems and big game hunting: models and application. *Biol. Conserv.* 142, 909–929.
- Cooley, H.S., Robinson, H.S., Wielgus, R.B., Lambert, C.M., 2008. Cougar prey selection in a white-tailed deer and mule deer community. *J. Wildl. Manage.* 72, 99–106.
- Cooley, H.S., Wielgus, R.B., Koehler, G., Maletzke, B., 2009a. Source populations in carnivore management; cougar demography and emigration in a lightly hunted population. *Anim. Conserv.* 12, 321–328.
- Cooley, H.S., Wielgus, R.B., Koehler, G.M., Robinson, H.S., Maletzke, B.T., 2009b. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology* 90, 2913–2921.
- Dwyer, J.F., 2009. Raptor electrocution: a case study on ecological traps, sinks, and additive mortality. *J. Nat. Resour. Life Sci. Educ.* 38, 93–98.
- Ebert, T.A., 1999. Plant and Animal Methods in Demography. Academic Press, San Diego, California, USA.
- Heisey, D.M., Fuller, T.K., 1985. Evaluation of survival and cause specific mortality rates using telemetry data. *J. Wildl. Manage.* 49, 668–674.
- Hornocker, M.G., 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildl. Monogr.* 21, 1–39.
- Lambert, M.S., Wielgus, R.B., Robinson, H.S., Katnick, D.D., Cruickshank, H.S., Clark, R., Almack, J., 2006. Cougar population dynamics and viability in the Pacific Northwest. *J. Wildl. Manage.* 70 (1), 246–254.
- Laundre, J.W., Hernandez, L., Strenbel, D., Altendorf, K., Lopez, C., Gonzalez, 2000. Aging mountain lions using gum line recession. *Wildl. Soc. Bull.* 28, 963–966.
- Logan, K.A., Sweanor, L.L., 2001. Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore. Island Press, Washington, DC, USA.
- McLellan, B.N., 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16, 141–156.
- Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* 21, 36–47.
- Murray, D.L., 2006. On improving telemetry-based survival estimation. *J. Wildl. Manage.* 70, 1530–1543.
- Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J., Borgerhoff Mulder, M., 1988. Reproductive success in lions. In: Clutton-Brock, T.H. (Ed.), *Reproductive Success*. The University of Chicago Press, Chicago, pp. 363–383.
- Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H., Caro, T. 2010. Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conservation Biology: Contributed Paper*.
- Packer, C. et al., 2009. Sport hunting, predator control and conservation of large carnivores. *PLoS ONE* 4 (6), e5941.
- Peek, J.M., 1986. A Review of Wildlife Management. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Pusey, Packer, 1994. Infanticide in lions: consequences and counterstrategies. In: Parmigiani, S., von Saal, F. (Eds.), *Infanticide and Parental Care*. Harwood, London, pp. 277–299.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecol. Appl.* 18, 1028–1037.
- Robinson, H.S. DeSimone, R. 2011. The Garnet Range Mountain Lion Study: Characteristics of a Hunted Population in West-central Montana. Final Report. Montana Fish, Wildlife & Parks. Helena, MT.
- Ross, P.L., Jalkotzy, M.G., 1992. Characteristics of a hunted population of cougars in southwestern Alberta. *J. Wildl. Manage.* 56, 417–426.
- Sinclair, Anthony R.E., Frycell, John M., Caughley, Graeme, 2006. *Wildlife Ecology, Conservation and Management*, second ed. Blackwell Publishing, Malden MA.
- Smith, McDougal, 1991. The contribution of variance in lifetime reproduction to effective population size in Tigers. *Conserv. Biol.* 5, 484–490.
- Spreadbury, B.R., Musil, K., Musil, J., Kaisner, C., Kovak, J., 1996. Cougar population characteristics in southeastern British Columbia. *J. Wildl. Manage.* 64, 962–969.

- Staines, B.W., 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). *J. Zool.* 184, 403–419.
- Stoner, D.C., Wolf, M.L., Choate, D.M., 2006. Cougar exploitation level in Utah; implications for demographic structure, population recovery and metapopulation dynamics. *J. Wildl. Manage.* 70, 1588–1600.
- Sweaner, Linda L., Logan, Kenneth A., Hornocker, Maurice G., 2000. Cougar dispersal patterns, metapopulation dynamics and conservation. *Conserv. Biol.* 14, 798–808.
- Swenson, J.E., 2003. Implications of sexually selected infanticide for the hunting of large carnivores. In: Festa-Bianchet, M., Apollino, M. (Eds.), *Animal Behavior and Wildlife Conservation*. Island Press, Washington, DC, USA, pp. 171–189.
- Swenson, J.E., Sandegren, F., Brunberg, S., Segerström, P., 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12, 69–80.
- Swenson, J.E., Sandegren, F., Soderberg, A., Bjarvall, A., Franzen, R., Wabakken, P., 1997. The infanticide caused by hunting of male bears. *Nature* 386, 450–451.
- Treves, Adrian., 2009. Hunting for large carnivore conservation. *J. Appl. Ecol.* 46, 1350–1356.
- Winterstein, S.R., Pollock, K.H., Bunk, C.M., 2001. Analysis of survival data from radiotelemetry studies. In: Millspaugh, J.T., Marzluff, J.M. (Eds.), *Radio Tracking and Animal Populations*. Academic Press, New York, New York, USA, pp. 353–380.
- White, Kevin 2009. Prey use by Male and Female Cougars in an Elk and Deer Community. MS Thesis. Washington State University.
- Wielgus, Robert.B., Sarrazin, F., Ferriere, R., Colbert, J., 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biol. Conserv.* 98 (3), 293–303.
- Wielgus, Robert.B., Bunnell, F.L., 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biol. Conserv.* 93, 145–154.
- Wielgus, Robert.B., Bunnell, F.L., 1995. Test of hypotheses for sexual segregation in grizzly bears. *J. Wildl. Manage.* 59, 552–560.
- Wielgus, Robert B., Bunnell, F.L., 1994a. Sexual segregation and female grizzly bear avoidance of males. *J. Wildl. Manage.* 58, 405–413.
- Wielgus, Robert.B., Bunnell, F.L., 1994b. Dynamics of a small hunted brown bear population in southwestern Alberta, Canada. *Biol. Conserv.* 67, 161–166.