

SINK POPULATIONS IN CARNIVORE MANAGEMENT: COUGAR DEMOGRAPHY AND IMMIGRATION IN A HUNTED POPULATION

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Abstract. Carnivores are widely hunted for both sport and population control, especially where they conflict with human interests. It is widely believed that sport hunting is effective in reducing carnivore populations and related human–carnivore conflicts, while maintaining viable populations. However, the way in which carnivore populations respond to harvest can vary greatly depending on their social structure, reproductive strategies, and dispersal patterns. For example, hunted cougar (*Puma concolor*) populations have shown a great degree of resiliency. Although hunting cougars on a broad geographic scale (>2000 km²) has reduced densities, hunting of smaller areas (i.e., game management units, <1000 km²), could conceivably fail because of increased immigration from adjacent source areas. We monitored a heavily hunted population from 2001 to 2006 to test for the effects of hunting at a small scale (<1000 km²) and to gauge whether population control was achieved ($\lambda \leq 1.0$) or if hunting losses were negated by increased immigration allowing the population to remain stable or increase ($\lambda \geq 1.0$). The observed growth rate of 1.00 was significantly higher than our predicted survival/fecundity growth rates (using a Leslie matrix) of 0.89 (deterministic) and 0.84 (stochastic), with the difference representing an 11–16% annual immigration rate. We observed no decline in density of the total population or the adult population, but a significant decrease in the average age of independent males. We found that the male component of the population was increasing (observed male population growth rate, $\lambda_{OM} = 1.09$), masking a decrease in the female component ($\lambda_{OF} = 0.91$). Our data support the compensatory immigration sink hypothesis; cougar removal in small game management areas (<1000 km²) increased immigration and recruitment of younger animals from adjacent areas, resulting in little or no reduction in local cougar densities and a shift in population structure toward younger animals. Hunting in high-quality habitats may create an attractive sink, leading to misinterpretation of population trends and masking population declines in the sink and surrounding source areas.

Key words: attractive sink; carnivore; cougar; hunting; immigration; mortality; population dynamics; *Puma concolor*; source–sink; survival.

INTRODUCTION

Carnivores are widely hunted for sport and population control, in part to reduce their effect on prey and to reduce conflicts with humans and their property (Treves and Karanth 2003). It is widely believed that sport hunting can be effective to reduce carnivore populations and related human–carnivore conflicts while maintaining viable populations (Strickland et al. 1994). How carnivore populations respond to harvest can vary greatly depending on their social structure, reproductive strategies, and dispersal patterns (Frank and Woodroffe 2001). Dispersal, in particular, can have significant ramifications (both stabilizing and destabilizing) on

population dynamics (Hanski 2001). Density-dependent dispersal may stabilize populations as immigration and emigration counterbalance between hunted (sink) and nonhunted (source) populations. However, many carnivore species display high levels of intrinsic dispersal of predominantly juvenile males, regardless of natal population density (Chepko-Sade and Halpin 1987, Zimmermann et al. 2005). Such intrinsic dispersal may mimic mortality if emigration is not reciprocated by immigration from neighboring populations, thereby greatly increasing the risk of sudden and dramatic decline in both source and sink populations (Howe et al. 1991). If carnivore management plans do not take into account the specific response of individual species and geographic scale of harvest, they may be more detrimental to the greater population than intended, or ineffective for local population control (Reynolds and Tapper 1996, Frank and Woodroffe 2001, Baker and Harris 2006).

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Cougars (*Puma concolor*) are widely hunted for both sport and population reduction in western North America (Cougar Management Guidelines Working Group 2005:71). Although high harvest during the 18th and 19th centuries caused local extinctions and reduced the species' range (Nowak 1976), some extant populations have sustained annual harvest levels of 15–30% of resident adults (Murphy 1983, Ross and Jalkotzy 1992). Other populations have rebounded quickly following single perturbations (Lindzey et al. 1992, Logan and Swenor 2001:171) or after harvest rates were lowered (Anderson and Lindzey 2005).

The resiliency of cougar populations is thought to depend on high levels of juvenile immigration from neighboring areas and philopatric recruitment of female offspring (Lindzey et al. 1992, Swenor et al. 2000). If such replacement or compensatory immigration occurs, localized hunting pressure may actually be ineffective or even counterproductive for population control. Although hunting cougars on a broad geographic scale (>2000 km²) can reduce cougar densities (Lambert et al. 2006), hunting of small areas (<1000 km²), as currently prescribed by many government agencies to reduce local populations and cougar–human conflicts (e.g., Oregon Department of Fish and Wildlife 2006:39, Wyoming Game and Fish Department 2006:19), may simply create a localized “sink,” a population characterized by its dependence on immigration to maintain stability (Pulliam 1988, Thomas and Kunin 1999). In cougar populations, younger individuals are most often involved in conflicts with humans (Beier 1991). High immigration and recruitment in sinks may shift the population structure toward younger animals, perhaps confounding the stated management goal of reducing cougar–human conflicts.

We tested the following hypotheses relative to the effects of hunting at a small scale (<1000 km²) to determine if hunting reduced population size, or simply created a sink with increased immigration. The hunting control (closed-population) hypothesis predicts that emigration and immigration are equal, that cougar harvest is an additive mortality source, and that harvest will reduce cougar densities in a given area. The compensatory immigration (metapopulation source–sink) hypothesis predicts that cougar removal in small areas will result in high levels of immigration and recruitment, resulting in little or no reduction in cougar densities and a shift in population structure toward younger animals. We intensively monitored a hunted cougar population in northeastern Washington State, USA from late 2001 to 2006 to determine overall population growth, male and female population growth, density, and age structure. To determine immigration rate, we compared the growth rates predicted by a standard closed-population survival/fecundity model (calculated from a Leslie matrix) based on radio-collar data, with growth rates determined from the total known/real open population.

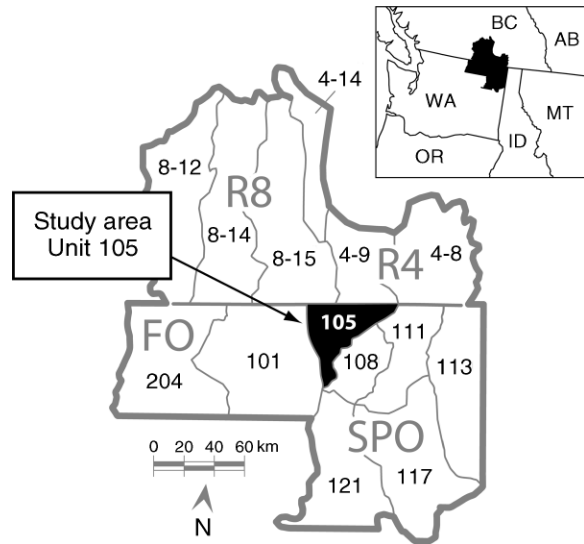


FIG. 1. Study area (Game Management Unit 105) surrounded by the Ferry-Okanogan (FO) and Stevens-Pend Orielle (SPO) cougar management zones of Washington State, USA, and by Region 4 (R4) and Region 8 (R8) of British Columbia (BC), Canada. Cougar management zones and Wildlife Regions are composed of smaller Game Management Units (i.e., 105, 8-15).

STUDY AREA

Our study was conducted in Washington State's Game Management Unit 105, an area of 735 km². This triangular-shaped mix of public (Colville National Forest) and private land is bounded to the north by the Canadian border, and to the east and west by the Columbia and Kettle rivers, respectively (Fig. 1). The area is located in the Northern Rocky Mountain (USA) Ecoprovince (Bailey 1995) and is characterized by rugged terrain with numerous ridges (1500–2000 m) interspersed by low valleys (500 m). Average winter temperature (November–March) is 4.2°C and average summer temperature (April–October) is 23.8°C. Precipitation averages 439 mm/yr, with the majority falling in winter. Between November and March there is an average of 8.6 cm of snow on the ground at an elevation of 500 m.

Mixed evergreen–deciduous forest dominates the landscape. Upland overstory species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), and subalpine fir (*Abies lasiocarpa*). At the lowest elevations and driest south-facing slopes, grasslands dominate, with some areas cleared and irrigated for alfalfa (*Medicago sativa*) production.

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. Populations of both species of deer, the main prey for cougars in the area, remained constant during the study period (Cooley et al. 2008). Common

predator species besides cougar include coyote (*Canis latrans*), black bear (*Ursus americanus*), and bobcat (*Lynx rufus*).

In 1996 the use of hounds to hunt cougars was banned in Washington State by public initiative. State wildlife officials tried to maintain hunting pressure on the population by increasing the “bag limit” from one to two animals for non-hound hunters and by making cougar hunting tags more accessible to the public. In 2000, in part because of increased public concern over cougar–human conflicts, Washington reinstated a limited hunt using hounds (Washington Substitute Senate Bill 5001). This “public safety cougar removal” targeted cougars in specific areas with numerous public complaints (Beausoleil et al. 2003). In 2004, an additional limited hound season was introduced in five counties in northern Washington (Washington Substitute Senate Bill 6118). Our study area was included in this new hound season as part of the Stevens-Pend Oreille cougar management zone that had a quota of 38 total cougars or 15 females. During the 2004–2005 season, 33 cougars were harvested before the female quota was reached and the season was closed. Cougar populations and harvest levels, including neighboring portions of British Columbia, have declined across the region since a peak between 1999 and 2001 (Lambert et al. 2006); see Fig. 2.

METHODS

Cougar capture

From December 2001 to April 2006, we attempted to radio-collar all cougars in the study area that were at least one year old, following the method first described by Hornocker (1970). Immobilized cougars were sexed, aged, and examined to gauge general health. Animals were fitted with numbered ear tags and either a VHF (Advanced Telemetry Systems, Isanti, Minnesota, USA) or GPS (Lotek Wireless, Newmarket, Ontario, Canada) radio collar equipped with mortality sensor on a 7-h delay. Age of adults was based on gum recession (Laundre et al. 2000). Young animals that did not show any gum recession were aged based on known birth date, size, pelage, movements, and social status. Cougar dispersal occurs between 10 and 33 months (Sweaner et al. 2000); therefore, animals still traveling with their mothers when first encountered were assigned an age of between 3 and 18 months based on their size. Animals traveling with siblings when collared, and independent animals that continued to disperse after being collared (establishing a home range distinct from their capture location), were assumed to be juveniles in the early stages of dispersal and were ascribed an age of 21 months. Independent animals that established a home range that included their capture location were assumed to have completed dispersal and were classified as subadults, assigned an age of 25 months.

All animals (collared and uncollared) that were shot in the study area as part of the sport harvest or as problem wildlife were sexed and aged during a

compulsory inspection by Washington Department of Fish and Wildlife staff. Hunters were required to provide intact proof of sex (genitalia) on cougar pelts no later than 5 days post harvest. A premolar was extracted as part of this compulsory inspection and was sent to the Matson Lab (Milltown, Montana, USA) for aging by analysis of cementum annuli. We performed a paired *t* test (estimated age of collared cougars by gum recession and by cementum annuli following harvest) to test for agreement between the two aging methods. Simple linear regression was used to examine the trend in age structure (Zar 1999:324).

Based on their age when collared or first observed, as in the case of kittens and juveniles, study animals were placed in one of the following four age categories: kittens (1–12 months), juveniles (13–24 months), subadults (25–36 months), and adults (≥ 37 months). Maximum age was set at 10 years or 120 months (see *Results*).

Survival

Cougars give birth year-round (Murphy et al. 1999:80, Logan and Sweaner 2001:88) and therefore do not fit the normal “birth pulse” method of calculating age-specific annual survival based on a calendar (e.g., January–January), or biological (e.g., June–June) year. 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 four months of radio-days to juvenile (13–24 months) survival and was assumed to become a subadult (25–36 months) in May, becoming an adult (37–48 months) the following May, and so on.

Annual age-specific survival rates were calculated based on daily survival rates (Heisey and Fuller 1985) by grouping all animals in each age category across the entire study period (December 2001 to August 2006). Radio-days of adult males were grouped from adult 4 years to adult 10 years, whereas female adult survival was divided into two categories, adult 4–5 years and adult 6+ years. This grouping was based on mortality sources and was used to reduce variance within groups. In a hunted population, males have an equal probability of mortality across their adult life (i.e., a 3-year-old male is as large, and therefore as desirable a trophy, as an 8-year-old male). Females, on the other hand, experience mortality causes beyond hunting that vary with age and reproductive status. Females with kittens suffer from intraspecific mortality in defense of their kittens and may sustain higher natural mortality rates as they mature (Logan and Sweaner 2001:129, Stoner et al. 2006). We used one-tailed, known-variance *z* tests to test if female survival was significantly higher than male survival and mortality rates.

No kittens were radio-collared during our study. Therefore kitten survival was based on the total number of kittens that survived divided by the total number born

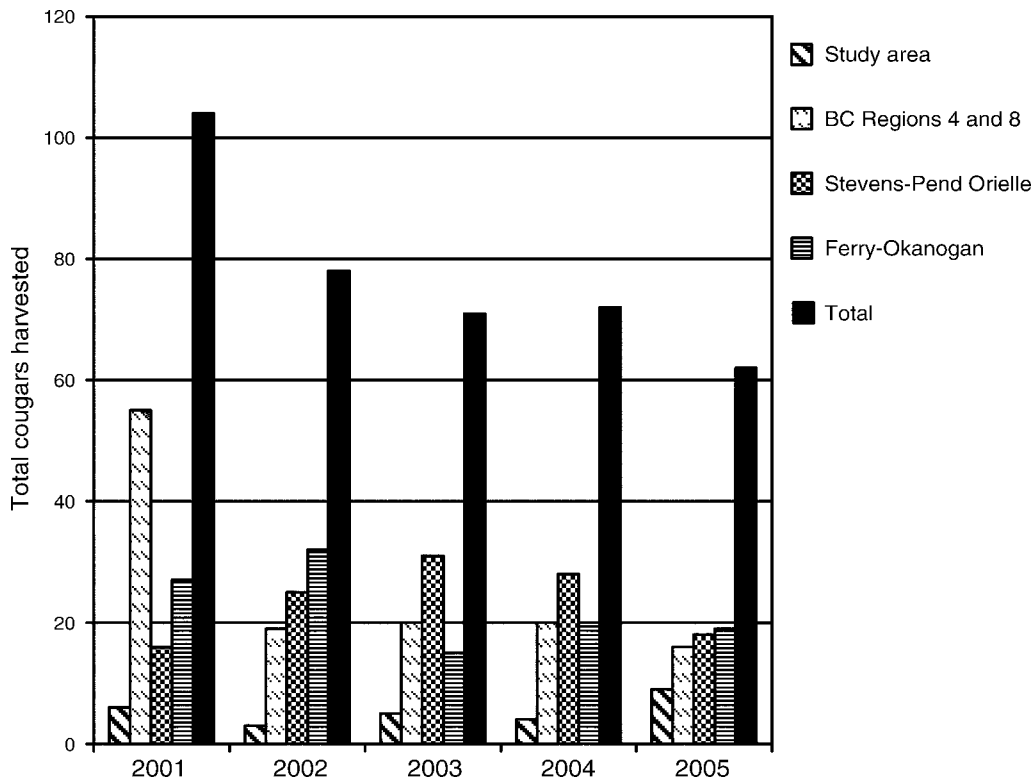


FIG. 2. Total cougar harvest (all ages and both sexes) for the years 2001–2005 in the study area and neighboring region, including Washington State's Ferry-Okanogan and Stevens-Pend Orielle Cougar Management Units and portions of British Columbia's Regions 4 and 8 (see also Fig. 1).

each year. A low estimate was based solely on den visits where the number of kittens born was known. Their survival rates were based on tracks observed traveling with collared females within one year of birth. This first estimate was considered to be biased low because of the small sample obtained ($n = 12$ kittens from five dens). The high estimate was based on kittens ≤ 1 year old observed traveling with collared females ($n = 19$ kittens). This second estimate is considered biased upward because the actual number of kittens born was not known and animals that died within 3–6 months of birth (before being detected) would not have been documented. We calculated the mean of the low and high estimates to obtain what we believe to be the least biased estimate of kitten survival.

Maternity and fecundity

Maternity (mean litter size per female per year) was the mean number of kittens observed, through both den visits and tracking, divided by the total number of females observed that year (Case 2000). Fecundity rates were calculated using the average maternity rates and average adult female survival (>24 months) $F = S_F \times M_{x+1}$ (the number of females that survive in year x multiplied by their mean maternity rate the following year) (Ebert 1999).

Deterministic and stochastic growth rates

We constructed a survival/fecundity dual-sex Leslie matrix (Leslie 1945) in RAMAS GIS (Akçakaya 2002) using the calculated survival and fecundity parameters. This closed-population model assumes that immigration and emigration balance and do not affect growth rate. Females were assumed to first breed as subadults (>24 months), and fecundity was kept constant for females aged 25 months and older (Anderson 1983). We used an equal sex ratio in kittens (Logan and Sweanor 2001:69) and all animals were assumed to die before reaching age class 11 years. Beier (1996) believed that cougars become senescent at age 12 and Lambert et al. (2006) also used this age in their cougar dual-sex matrix. Furthermore, in a heavily hunted population in Wyoming, Logan et al. (1986) found few cougars ≥ 7 years old and we found no adults >9 years old in our study area (see *Results*). Deterministic population growth rate (λ_D) was derived from the Leslie matrix.

To calculate a stochastic growth rate, we used annual environmental variation in population parameters (standard deviation of survival and fecundity). Rates were calculated for each year of the study based on an August–August year. Because of small sample sizes for each sex and age class (not all age classes were present in each year), standard deviations of survival rates were calculated by pooling all age classes for each sex in each

TABLE 1. Radio-days, total mortality, and survival rate (mean \pm SD) by sex and age class for 34 radio-collared cougars (*Puma concolor*) in northeast Washington State, USA, 2002–2006.

Age class	Females			Males		
	No. radio-days	No. dead	Survival rate	No. radio-days	No. dead	Survival rate
Juvenile (13–24 months)	698	1	0.5926 \pm 0.31	785	1	0.6280 \pm 0.29
Subadult (25–36 months)	2039	1	0.8360 \pm 0.15	1083	2	0.5093 \pm 0.24
Male adult 4+ (37–108 months)				1018	3	0.3405 \pm 0.21
Female adult 4–6 (37–60 months)	3530	3	0.7332 \pm 0.13			
Female adult 6+ (61–108 months)	1883	2	0.6785 \pm 0.19			
Total (all ages)	8150	7	0.7308 \pm 0.09	2886	6	0.4678 \pm 0.15

year. Annual variation in survival, and therefore fecundity, was assumed to affect each age class equally.

An average stochastic growth rate was obtained by running 300 four-year (three-transition) population trials based on the same population parameters used in the deterministic model, but with annual environmental and demographic variation represented in a standard deviation matrix (Akçakaya 2002).

Observed growth rate

We back-calculated the life span of all cougars known to have spent time in the study area from August 2001 to August 2005 using methods described by Logan and Sweanor (2001:66) and Stoner et al. (2006). This form of census includes all population constituents, including immigrants.

Males and females were backdated differently based on their distinct dispersal patterns; males disperse a long distance from their natal home ranges, whereas females display much shorter dispersal distances, often establishing philopatric home ranges within or adjacent to their mother's range (Sweanor et al. 2000, Logan and Sweanor 2001:236, Stoner et al. 2006). Males were assumed to have immigrated into the study area at 21 months of age. Therefore, independent males that were older than 21 months when first encountered were assumed to have been present in the study area from 21 months of age. Independent females older than 21 months were assumed to have been born in the study area or to have resided in it since August 2001, whichever came first. Kittens were assumed to be present at one month of age. Juveniles and kittens traveling with adult females that were not decisively sexed or collared were divided equally between sexes (Logan and Sweanor 2001:69).

Independent animals that were treed but not collared or only had their tracks observed were not included in the population estimate because of the risk of double-counting individuals. For example, an animal that was treed but never marked may have been later harvested or captured in the study area and therefore included in the population estimate twice. This method therefore yields a minimum population estimate.

The observed population growth rate (λ_O) and sex-specific female and male growth rates (λ_F and λ_M) were determined based on the total number of cougars (adults

and kittens) each year using the formula $\lambda_x = (n_t/n_0)^{1/t}$, 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 2000:3).

Comparison of population growth rates

A one-tailed, one-sample t test was used to test if deterministic (λ_D) and stochastic (λ_S) growth rates were lower than the average four-year observed (λ_O) growth rate (Zar 1999:96). Immigration rate (i) was estimated by comparing the survival/fecundity model growth rates to the observed/real growth rate using the equations $i = \lambda_O - \lambda_D$ and $i = \lambda_O - \lambda_S$ (Peery et al. 2006).

Population density

We calculated density based on the total number of cougars present in the study area over the course of each year (Ross and Jalkotzy 1992, Spreadbury et al. 1996). This method may not be extrapolated to areas outside the study area, but provides a consistent measure of density among years. Simple linear regression was used to test for significant changes in density over the study period (Zar 1999:324).

RESULTS

Cougar capture

Seventy-nine animals were observed in the study area between August 2001 and August 2005. We collared 34 cougars: 19 juveniles (12 males, seven females), four subadults (two males, two females), and 11 adults (two males, nine females); see Table 1. Nineteen uncollared cougars were shot in the study area: eight females (two juveniles, three subadults, and three adults) and 11 males (two juveniles, five subadults, and four adults). Twenty-four kittens (six males, nine females, and nine unknowns) and two juveniles (one male and one female) were observed traveling with collared females but were never collared. Age determined by gum recession was not significantly different than age determined by cementum annuli in 14 samples for which both methods were used on a single animal ($t = 0.39$, $df = 13$, $P = 0.70$).

Survival and mortality

Hunting was the main cause of mortality within the population, accounting for nine of 13 deaths of study

TABLE 2. Sources and rates of mortality (mean \pm SD) and number of dead animals (in parentheses) by sex and age class for 34 radio-collared cougars in northeast Washington, 2001–2006.

Sex and age class	Mortality source		
	Depredation	Hunting	Natural
Female			
Juvenile (12–24 months)			0.4074 \pm 0.31 (1)
Subadult (25–36 months)		0.1639 \pm 0.15 (1)	
Adult 4–6 (37–60 months)		0.1778 \pm 0.11 (2)	0.0889 \pm 0.08 (1)
Adult 6+ (61–120 months)		0.1607 \pm 0.14 (1)	0.1607 \pm 0.14 (1)
Female total		0.1538 \pm 0.07 (4)	0.1153 \pm 0.06 (3)
Male			
Juvenile (12–24 months)		0.3720 \pm 0.29 (1)	
Subadult (25–36 months)		0.4906 \pm 0.24 (2)	
Adult 4+ (37–120 months)	0.2198 \pm 0.19 (1)	0.4396 \pm 0.23 (2)	
Male total	0.0887 \pm 0.08 (1)	0.4434 \pm 0.14 (5)	
Population total	0.0268 \pm 0.02 (1)	0.2420 \pm 0.07 (9)	0.0806 \pm 0.04 (3)

animals (hunting mortality rate = 0.24; Table 2). Three cougars died of natural causes (natural mortality rate = 0.08), and one adult was killed in a depredation hunt when he was found to be killing domestic sheep (annual depredation mortality rate = 0.02). Four males emigrated and were censored to their last known date in the study area. Three females either shed their collars or went missing after being collared; two adults died during capture and were censored from the data.

Thirty-one cougars were first encountered as kittens (18 were assumed or known to survive to dispersal). Combining high (0.74) and low (0.44) survival estimates for each year produced an annual kitten survival rate of 0.59 ± 0.21 (mean \pm SD). When age classes were pooled for each sex, females had a higher probability of survival than males ($S_F = 0.73$ vs. $S_M = 0.47$, $Z = 1.55$; $df = 1$, $P = 0.06$), mostly the result of higher hunting mortality (female hunting mortality rate = 0.15 vs. male hunting mortality rate = 0.44, $Z = 1.79$; $df = 1$, $P = 0.04$) (Tables 1 and 2).

Maternity and fecundity

Mean maternity was 1.20 kittens per female per year. Annual survival of reproducing-aged females (25+ months) was 0.74 ± 0.09 (mean \pm SD). These combined rates create an annual fecundity rate of 0.45 ± 0.35 for each sex of kitten.

Population growth rates

The deterministic annual growth rate (λ_D) based on our survival and fecundity model was 0.89. The stochastic annual growth rate (λ_S) including the standard deviations of survival and fecundity was 0.84 ± 0.21 (mean \pm SD). The observed growth rate (λ_O) based on the actual number of cougars in the study area was 1.00 ± 0.07 . Both of our modeled growth rates were significantly lower than the observed rate (for λ_D , $t = 2.42$, $df = 2$, $P = 0.07$; for λ_S , $t = 3.68$, $df = 2$, $P = 0.03$).

The observed male component of the population grew at 9% annually, ($\lambda_{OM} = 1.09$), whereas the observed

female component declined at the same rate ($\lambda_{OF} = 0.91$). The observed female growth rate was very similar to the population's deterministic annual growth rate ($\lambda_D = 0.89$).

Population density

Total cougar density averaged 5.03 animals/100 km² and did not change significantly over the study period (see Fig. 3; $F = 0.06$, $P = 0.82$, $R^2 = 0.03$; for all regressions, MS regression $df = 1$; MS residual $df = 2$). Density of adult (>24 months) males appeared to increase, although not significantly, from five individuals in 2001 or 0.68/100 km² to nine individuals in 2005 or 1.22/100 km² ($F = 1.66$, $P = 0.33$, $R^2 = 0.45$), while adult female density remained constant between 13 individuals or 1.77/100 km² and 10 individuals or 1.36/100 km² ($F = 0.71$, $P = 0.49$, $R^2 = 0.26$). The total adult density (males and females >24 months) also remained constant ranging from 17 individuals or 2.32/100 km² in 2001–2002 to 19 individuals or 2.58/100 km² in 2004–2005 ($F = 1.11$, $P = 0.40$, $R^2 = 0.36$).

Age structure

The mean age of the total population was 26 months, adult males 41 months, and adult females 46 months. The average age of independent adult males (>24 months) declined significantly from 47.8 months in 2001 to 36 months in 2005 (see Fig. 4; $F = 37.81$, $P = 0.02$, $R^2 = 0.95$; for all regressions, MS regression $df = 1$; MS residual $df = 2$). The average age of independent females increased, although not significantly, from 42.5 to 54.3 months over the study period ($F = 7.99$, $P = 0.11$, $R^2 = 0.80$).

DISCUSSION

Our closed population survival/fecundity models predicted a rapidly declining cougar population within the study area ($\lambda_D = 0.89$, $\lambda_S = 0.84$), whereas the observed/real population remained stable ($\lambda_O = 1.00$). The real growth rate of 1.00 was significantly higher

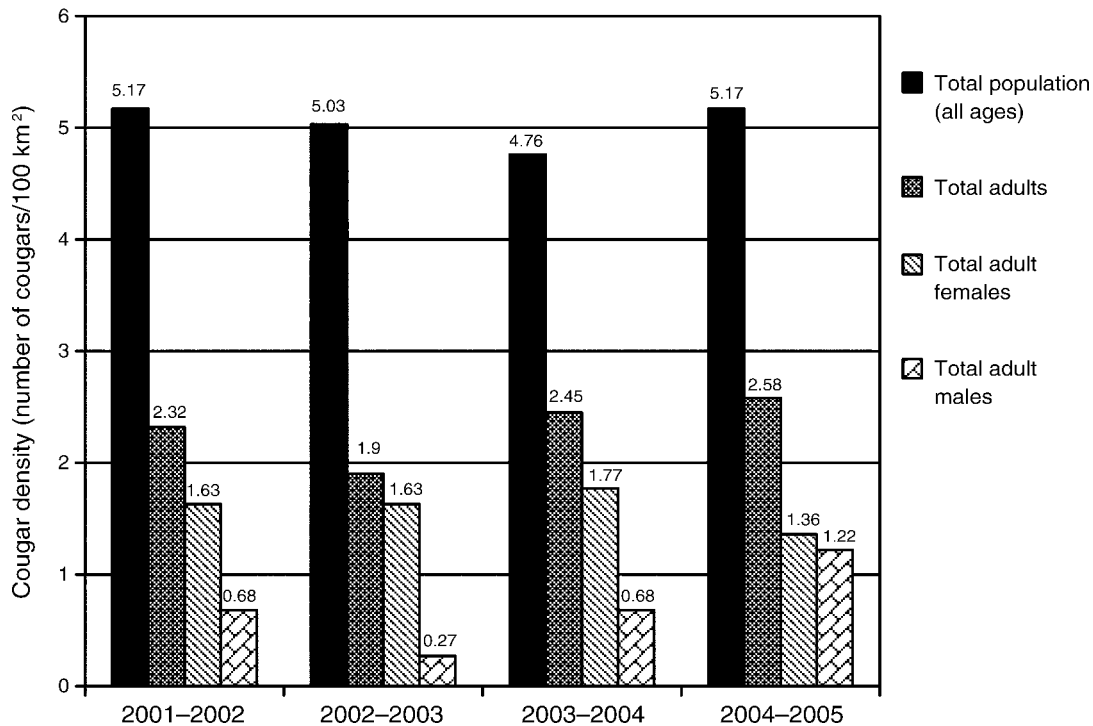


FIG. 3. Total and adult cougar (>24 months old) densities (density values given above bars) within the study area in northeastern Washington State, August to August 2001–2005.

than both the modeled deterministic growth rate λ_D and the stochastic growth rate λ_S , the difference representing an 11–16% annual immigration rate. Immigration was also evidenced by no decline in the total or adult population densities, a shift toward males in the adult population (the adult male component of the population was increasing at 9% per year while the female component was declining), and a significant decrease in the average age of independent males. Our results reject the closed-population hunting control hypothesis and support the open-population compensatory/sink immigration hypothesis, which holds that cougar removal in small areas (<1000 km²) will produce high levels of immigration, resulting in little or no reduction in cougar density and a shift in population structure toward younger animals.

The high immigration rates (11–16%), and the disparate growth rates of the male and female components of the population (0.91 female and 1.09 male) suggest that our study area is acting as a sink for the surrounding area. Without immigration of a large number of mostly male cougars, the population would be declining close to the rate predicted by our population models. Immigration into our study area is occurring despite declines in the surrounding area (Fig. 2), due to the intrinsic nature of dispersal in cougar populations.

How far a dispersing animal will travel before establishing a home range is reliant on the quality of

habitat and the number of available mates (Waser 1996:289). Carnivore densities are positively correlated with prey biomass (Hanby et al. 1995, Carbone and Gittleman 2002). High levels of prey availability will cause an increase in the presence of transient or immigrant animals, and may also increase reproduction and survival of neonates and juveniles from within the population (Fuller and Sievert 2001:170). Although male cougars disperse long distances to avoid inbreeding, females disperse to avoid intraspecific competition (Logan and Sweanor 2001:242). As a result, males disperse, on average, twice the distance of females, independent of natal home range density (intrinsic dispersal). High prey availability may be resulting in high immigration of transient animals. We believe that both males and females are immigrating into the study area, although males immigrate on a more constant annual basis, as reflected in the increasing ratio of males to females in the adult population. Data from collared animals suggest that immigrant females have a higher survival rate than males and thus are propagated through the population, whereas males are hunted as juveniles and subadults (Table 2).

Hunting pressure that is not evenly distributed across the landscape has been shown to induce source-sink dynamics in carnivore populations (Doak 1995, Slough and Mowat 1996, Novaro et al. 2005). Hunting is a form of habitat degradation that cannot be perceived by dispersing animals, leading to what Delibes et al. (2001)

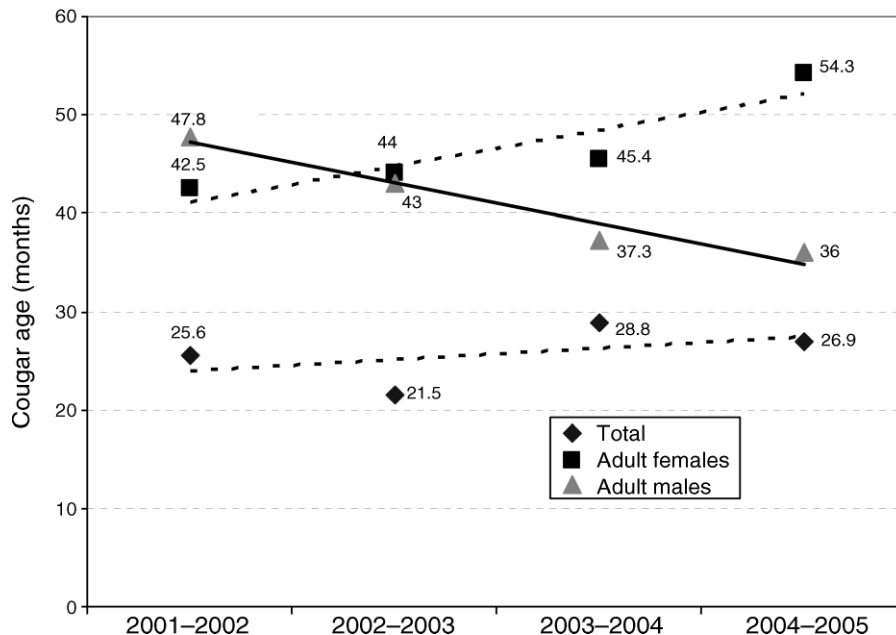


FIG. 4. Mean age (values given next to symbols) of the total population, independent adult females (>24 months old), and independent adult males (>24 months old) of a cougar population in northeastern Washington State, 2001–2005 (a solid line denotes a significant [$P < 0.05$] regression for adult males; dashed lines are nonsignificant). Age is based on each animal's average age from August to August of each year.

termed “attractive sinks”; habitat patches of disparate mortality that would otherwise provide abundant resources and high reproduction. When attractive sinks are the preferred habitat, their effect on the greater population is dramatic. The ratio of sink to source habitat sets a threshold above which the total population declines sharply. This threshold is lowered with a decline in sink growth rate. For example, a decline in λ_{sink} from 0.9 to 0.7 results in the lowering of the threshold from 50% to 25% of the greater landscape needing to consist of sink habitat in order for the greater population to decline (Delibes et al. 2001). Depending on other demographic parameters (i.e., initial densities), declines in population may not affect sources and sinks simultaneously. In fact, sink populations may increase while source populations decline (Delibes et al. 2001).

Our study area was a single game management unit (GMU 105, total area 735 km²) within part of the larger Stevens-Pend Orielle cougar management zone (total area 9131 km²) (Fig. 1). Although the harvest quotas are set for the entire management zone, not all areas within that zone are hunted equally due to cougar densities, road access, and snow conditions (Barnhurst 1986, Diefenbach et al. 2004). Total harvest has declined since 2003 in the Stevens-Pend Orielle cougar management zone and earlier (2001) in the greater area (Fig. 2). Although harvest has declined outside the study area, possibly denoting a decline in the greater population (see also Lambert et al. 2006), it has remained constant or increased within the study area while the population has

remained stable. It would appear that metapopulation source-sink population dynamics are functioning within the scale of this single cougar management zone, with some local populations declining while others remain stable. Because males disperse regardless of natal home range density, the surrounding areas need not contain growing or even stable populations to act as a source. An increase in the male cougar population within our study area in response to heavy hunting pressure may be masking a decline in females in the same area and contributing to an overall decline in the greater population. Regardless of the effect on the greater population, it is clear that targeted reductions in small areas will be ineffective as long as habitat quality remains high and source populations exist.

Management implications of carnivore immigration into sink populations

Our findings have two management implications: (1) immigration from neighboring areas may counter management goals of carnivore reduction in small areas, and (2) even within large management zones, population reductions are unlikely to affect the entire region equally, with local immigration possibly masking a declining female population in the target area and an overall decline in the greater area. A similar phenomenon was observed in a heavily hunted brown bear (*Ursus arctos*) population, whereby an apparently increasing population was actually declining toward extirpation (Wielgus and Bunnell 1994).

Making informed management decisions regarding carnivore populations requires that we accurately assess their abundance and population growth rates. Like many other carnivore species, cougar populations are difficult to quantify; therefore, management is often based as much on public perception as on scientifically gathered census data (Minnis 1998). However, the public's perception of wildlife populations often runs counter to that of the scientific community (Freddy et al. 2004). Hunting pressure is often concentrated in areas that have the highest habitat quality and therefore the highest cougar densities. Our findings show that these same areas probably act as sinks, maintaining stable populations through increased immigration from surrounding source areas. If population estimates are based on these heavily hunted sink populations, off-take of recent immigrants could produce the illusion of a growing population in the greater region. However, pre- and post-hunting population densities vary greatly (Anderson and Lindzey 2005) as cougars are quickly replaced by high recruitment. High recruitment, in turn, could lead to public perception of strong population growth and pressure to increase harvest levels. This scenario quickly leads to what Logan and Sweaner (2001:373) describe as the "sledgehammer approach," in which cougar harvest rates are set by crude population indices such as hunter testimony, and populations are well into decline before hunting pressure is reduced.

Targeted reductions of cougar populations in small areas are currently a popular management strategy; however, our data suggest that these reductions may be ineffective if habitat quality remains high or if a source population exists. Reductions employed toward the management goals of reducing predation pressure may be confounded by high recruitment, while cougar-human conflicts may be exacerbated by the influx of younger animals. Ultimately, management aimed at population reduction must address the level of mobility and immigration of the target species. If hunting pressure can be employed uniformly across the landscape, immigration may be lowered by reducing the total population and therefore the number of source populations. This would require much more intense management of carnivores than is presently prescribed by many jurisdictions. Conversely, reducing habitat quality in the smaller targeted area may remove the appeal of an attractive sink, thereby reducing immigration. Sinclair and Krebs (2003) conclude "Food supply is the primary factor determining growth rate in animal populations, and we postulate bottom-up control as the universal primary standard." Others have suggested that prey reduction may provide a viable strategy in carnivore management (e.g., Robinson et al. 2002, Packer et al. 2005). The efficacy of "bottom-up" approaches to cougar management (alternate strategies aimed at reducing prey numbers) remains largely unexplored. We encourage others to study whether such methods may prove viable and appropriate for small management areas.

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