

Cougar Population Dynamics and Viability in the Pacific Northwest

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Abstract

Increasing reports of human/cougar conflicts may suggest that cougars are increasing in the Pacific Northwest. We determined minimum relative densities and average fecundity, survival, and growth rate of an apparently increasing cougar population in northeastern Washington, USA; northern Idaho, USA; and southern British Columbia, Canada, from 1998 to 2003. Minimum relative densities declined from 1.47 cougars/100 km² to 0.85 cougars/100 km². We estimated average litter size at 2.53 kittens, interbirth interval at 18 months, proportion of reproductively successful females at 75%, and age at first parturition at 18 months for a maternity rate of 1.27 kittens/adult female/yr. Average survival rate for all radiocollared cougars was 59%: 77% for adult females, 33% for adult males, 34% for yearlings, and 57% for kittens. Hunting accounted for 92% of mortalities of radiocollared cougars. The annual stochastic growth rate of this population was $\lambda = 0.80$ (95% CI = 0.11). Contrary to accepted belief, our findings suggest that cougars in the Pacific Northwest are currently declining. Increased conflicts between cougars and humans in this area could be the result of the 1) very young age structure of the population caused by heavy hunting, 2) increased human intrusion into cougar habitat, 3) low level of social acceptance of cougars in the area, or 4) habituation of cougars to humans. To help preserve this population, we recommend reduced levels of exploitation, particularly for adult females, continuous monitoring, and collaborative efforts of managers from adjacent states and provinces. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):246–254; 2006)

Key words

age-sex-structured model, British Columbia, carnivore, cougar, fecundity, Idaho, minimum density, population dynamics, Puma concolor, survival, viability analysis, Washington.

Cougar (*Puma concolor*) populations are believed to be increasing throughout western North America (Riley and Malecki 2001), as evidenced by the increased frequency of reported human/cougar encounters or complaints (Beier 1991, Chester 2003) and increasing numbers of cougar harvested (Dawn et al. 2003). This is especially true in Washington, USA, where harvest regulations have recently changed amid much controversy (Martorello 2003). Although bounties for predators were abolished in 1960, the number of cougars hunted in the state during the past century has increased (Spencer et al. 2001). Hunting with hounds became illegal in 1996 after voter Initiative 655 was passed, but the hunting season's length and bag limit were both increased to compensate for any decline in harvest. The years following Initiative 655 were marked by an increase in the number of human/cougar conflicts—annual registered complaints rose from 247 in 1995 (the year before the ban) to 495 in 1996 and 927 in 1998 (Washington Department of Fish and Wildlife 1999). Because of these complaints, Engrossed Substitute Senate Bill (ESSB) 5001 was passed in 2001, allowing the use of hounds for

cougar removals related to public safety concerns. The 2001 Washington game status report (Martorello 2001) suggested that cougars were stable or increasing statewide and were moderately exploited, so hunting regulations have continued to become more permissive. To further satisfy local safety concerns, emergency cougar hunts were adopted in March 2003 in Stevens, Ferry, and Okanogan counties in northeastern Washington, USA. Recent reports from neighboring Idaho, USA (Nadeau 2003), and British Columbia, Canada (Austin 2003), showed that hunting effort has also increased, with harvest levels in Idaho, USA, as much as 700% higher than 20 years ago.

Many hypotheses have been proposed to account for the increased number of cougar complaints in Washington. The most popular belief is that more frequent complaints indicate an increasing cougar population. Alternatively, encroachment of expanding suburbs into cougar habitat could be a cause (Spencer et al. 2001, Dickson and Beier 2002). However, hunting itself could also be indirectly responsible for the increased frequency in cougar/human conflicts. Carnivore populations under heavy hunting pressure may have a younger age structure than nonhunted populations, as seen in African lions (*Panthera leo*; Smuts 1978) and wolves (*Canis lupus*; Jedrezejewska et al. 1996). Removing

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older animals can cause social disruption (M. E. Sunkuist, University of Florida, unpublished data) and increase the numbers of immigrating/settling juveniles or young-adults from adjacent areas (Wielgus et al. 2001). Juveniles and young adults are responsible for most attacks on humans and livestock (Beier 1991). Finally, low levels of public acceptance of cougars, or cougar habituation to humans, can amplify the perception that cougars are increasing (Riley and Decker 2000, Riley and Malecki 2001), and the large number of complaints could be a local backlash to Initiative 655. Recent essays about cougar attacks (Deurbrouck and Miller 2001, Etling 2001, Baron 2003) could have contributed as well to raising public apprehensiveness of cougars.

The objective of this study was to test the hypothesis that cougars are increasing by determining growth rate of the population and corresponding trends, if any, in minimum relative density in northeastern Washington, USA; northern Idaho, USA; and southern British Columbia, Canada, between 1998 and 2003. We examined the demographic rates of 32 radiocollared cougars in the Selkirk Mountains in northern Idaho, USA (Panhandle area); southeastern British Columbia, Canada (Kootenay region); and northeastern Washington, USA (Pend Oreille County), between 1998 and 2001, and of 21 other cougars in the Colville National Forest in northeastern Washington (Ferry and Stevens counties), USA, between 2002 and 2003. Seven animals from the Selkirks were monitored throughout the study.

Study Area

The study area was located in the Northern Rocky Mountain, USA, ecoprovince (Bailey 1995) and the Southern Interior Mountains of British Columbia, Canada (Demarchi 1996; Fig. 1). The area was characterized by rugged terrain with numerous ridges (1,500–2,000 m) interspersed by valleys (500 m). Average winter temperature was 0°C, and the average summer temperature was 22°C. Precipitation fell mostly in the winter and averaged 510 to 1,020 mm per year.

Mixed evergreen–deciduous forest dominated the landscape. In

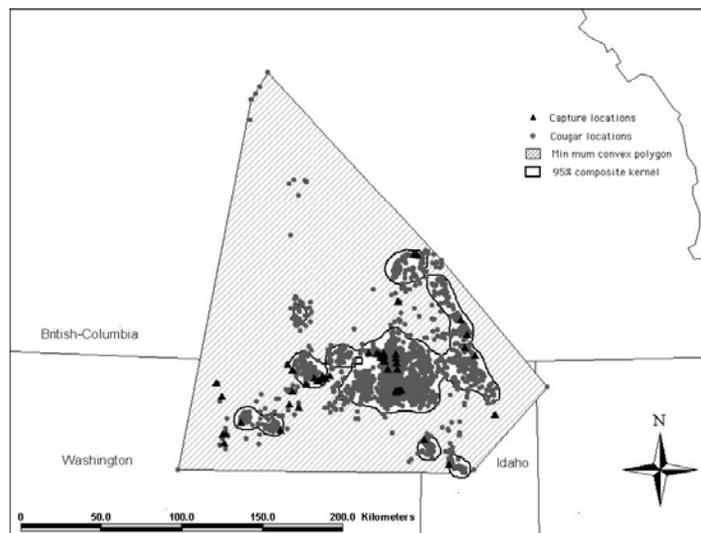


Figure 1. Study area in the Pacific Northwest, USA. Blank and hatched polygons represent the 95% adaptive kernel and minimum convex polygon composite home ranges of all cougars monitored from 1998 to 2003.

lower elevations, western red-cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) were the dominant tree species in mature forests, with black cottonwood (*Populus balsamifera trichocarpa*) in poorly drained areas. Open, mixed stands of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) were common on more xeric south-facing slopes (Ketcheson et al. 1991). At higher elevations, white spruce (*Picea glauca*) dominated the forest, with subalpine fir (*Abies lasiocarpa*) composing the understory and lodgepole pine (*Pinus contorta*) common in recently burned areas (Coupe et al. 1991).

White-tailed deer (*Odocoileus virginianus*) were the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and mountain caribou (*Rangifer tarandus caribou*) were also present (Katnik 2002, Robinson et al. 2002). Common predator species, beside cougar, included coyote (*Canis latrans*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), and, to a lesser extent, grizzly bear (*Ursus arctos*), lynx (*Lynx canadensis*), and wolf (*Canis lupus*).

Cougar harvest was permitted throughout the study area, but regulations varied among jurisdictions. In Washington, USA, the hunting season was 1 August to 15 March from 1998 to 2003. Hounds were prohibited in 1996, but their use was allowed after 2000 to meet public safety concerns. In Idaho, USA, the hunting season was 15 September to 31 March from 1998 to 2000, and 30 August to 31 March from 2000 to 2003. Excluding 1998, hounds were permitted from December to March (dates varied slightly among years). In British Columbia, Canada, cougar hunting with hounds was permitted in the southeastern Kootenay region from 10 September to 28 February and until 31 March in the southwestern Kootenays.

Methods

Capture and Monitoring

We searched the study area for cougar tracks in snow each year (Nov to Apr) from 1998 to 2003. Hounds were released on fresh tracks and used to tree cougars (Hornocker 1970) >30 kg (yearlings and adults). We immobilized treed cougars that were ≤5 m from the ground by injecting 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, with a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). We fitted cougars with mortality-sensing very high frequency (VHF) radiocollars and classified them either as kitten (0–1 yr), yearling (1–2 yr), or adult (2+ yr), based on their general appearance and tooth wear (Ashman and Greer 1976). We administered yohimbine hydrochloride to the captured animals (0.2 mg/kg of body mass) as a chemical antagonist of the xylazine hydrochloride (Seal et al. 1987). All animals were handled in accordance with Washington State University Animal Care Permit (IACUC) Number 3133. We located instrumented cougars about once a week by aerial or ground telemetry from 14 December 1998 to 20 May 2003 and determined ground locations with triangulation using LOAS (Ecological Software Solutions, Urnäsch, Switzerland).

Trends in Minimum Density and Abundance

We estimated minimum mean annual density of all cougars and of adults only (cougars/100 km² and adults/100 km²) in the study

area by counting all captured and monitored animals in the annual 95% adaptive-kernel composite home range of all adult females, using the animal movement extension in program ArcView® (ESRI, Redlands, California; Hooge and Eichenlaub 1997). This method has been used in other carnivore studies (Wielgus and Bunnell 1994, Wielgus et al. 1994, Wielgus and Bunnell 2000, Hellgren et al. 2005) and assumes that all cougars present were captured in the female composite home range. Because our capture efforts were limited by workforce, constrained by weather (winter only), concentrated along roads, and not distributed evenly (in time and space) in the study area (Fig. 1), this assumption was most likely violated. Therefore, our density estimates should not be considered as absolute real densities but, rather, as relative minimum densities, to be used only as corroborative evidence to track trends in relative density among years. We chose to exclude males and younger cougars from deriving the composite home range because 1) males had larger home ranges and were often in outer areas where we could not detect and monitor all females, and 2) younger cougars were often with their mothers, so their inclusion in the composite home range would have resulted in pseudoreplication. Densities of adult females were determined as the number of adult females divided by the composite home-range area. For adult males and yearlings (both sexes), we used 2 techniques. The first method summed the animals that were monitored each year, divided by the area of the adult female composite home range. The second method, also used for kitten density, was based on survival and fecundity rates and used the stable age distribution (dominant right eigenvector, [SAD]; Morris and Doak 2002:222) to determine the annual proportion of adult males, yearlings, and kittens that we would expect if the demographic rates of this population were constant. We then multiplied annual female densities in the composite home range by the corresponding male, yearling, or kitten fraction of the population to establish their respective densities. The SAD method assumes a stable age and sex structure of the population, which was uncertain for our studied population because our data covered only 5 years, but it allowed collateral density estimates for categories in which we had fewer animals monitored (adult males, yearlings, kittens). Because of the lack of population closure and because we wanted to use a realistic initial abundance in our population viability analysis (PVA), average cougar abundance in the study area was obtained by extrapolating the average annual minimum-density estimate over the minimum convex polygon (MCP) of all studied animals rather than over the smaller 95% adaptive-kernel, composite home range.

Fecundity

Maternity rates (m_x) were the average number of kittens of each sex (m_{xm} , m_{xf}) produced during 1 year by any mother of age x (Case 2000). Because cougars can reproduce all year long (birth-flow population), we conducted frequent checks of potentially reproductive females. We determined the reproductive status of females at capture by examining lactation, color and size of the nipples (to detect previous maternities), and presence of kittens or yearlings. Subsequent changes in the reproductive status were detected by weekly telemetry locations. We investigated a decrease in a female's movements that lasted longer than 10 days (approximately the maximum time spent at kill sites) as a possible

birth event (Hemker et al. 1986, Beier et al. 1995) and determined litter size by investigating dens or by track counts (Banhurst and Lindzey 1989, Ross and Jalkotzy 1992, Kerley et al. 2002). We calculated annual maternity rates (m_x) by dividing the average litter size by the average successful interbirth interval (in yr units) and multiplying by the proportion of kittens of each sex and the proportion of reproductively successful adult females (i.e., pregnant or involved in raising a litter). The latter parameter was used in calculating maternity rates because failing to consider the proportion of unsuccessfully reproducing females would bias kitten production upward by including only reproductively successful females during short study periods (Wielgus et al. 2001). Fecundity rates (F_x) of our postbreeding model were defined as $F_x = m_{x+1} \times S_{xf}$ (Case 2000), where m_{x+1} is the maternity rate of the next age class, and S_{xf} is the annual survival rate of females of age x . We assumed F_x had the same standard deviations as S_{xf} (see below) because sample sizes were too small to estimate the standard deviations for fecundity. This would likely result in underestimates of the standard deviations and in conservative estimates of population decline because standard deviations of survival should be smaller than standard deviations of the product of survivals and maternities.

Survival

We determined the survival of kittens by comparing direct observations or track counts on snow (Ross and Jalkotzy 1992, Kerley et al. 2002) at different time intervals. Because we could not monitor kittens daily, we evaluated their survival rate as the proportion of known survivors after the first year of life (365 d).

To estimate survival of radiocollared animals, we used the Mayfield method (1961) modified by Heisey and Fuller (1985) because of its high precision when demographic rates are constant within time intervals π (Samuel and Fuller 1996, see next paragraph). We estimated average annual survival rates by using the geometric mean of all years,

$$\left(\prod_{t=1}^Y S_t\right)^{1/Y},$$

where t represents each year of the study, Y the total number of years, and S_t the annual survival rates. We computed a 95% confidence interval with Akçakaya's (2002) unbiased weighted variance,

$$\frac{\sum_{t=1}^Y S_t(1 - S_t)}{\sum_{t=1}^Y n_t},$$

where n_t is the annual number of cougars monitored in each class. This variance estimate minimizes sampling error and accounts for demographic stochasticity (Akçakaya 2002).

To meet the required assumption of constant mortality of the Mayfield method, we analyzed the statistical distribution of the deaths over a year (365 d) to determine the time intervals when survival probabilities were constant. This yielded 2 seasons: the high mortality (HM) season (13 Nov to 20 May) and the low mortality (LM) season (21 May to 12 Nov; Fig. 2). Most of the

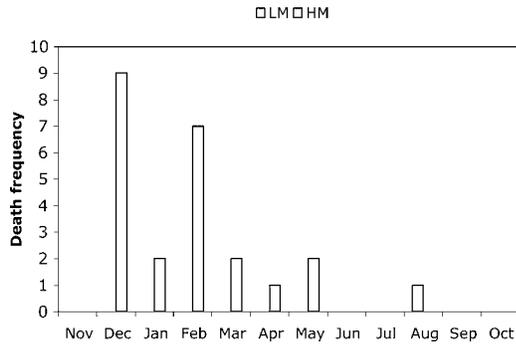


Figure 2. Monthly distribution of the cougar mortalities in the Pacific Northwest, USA, from 1998 to 2003. High mortality (HM) season was from 13 November to 20 May and low mortality (LM) season was from 21 May to 12 November. Seasons were defined by the median date of the deaths and were used to meet the assumption of constant mortality within each time interval required by the Heisey-Fuller survival analysis.

deaths (22 of 23) during the HM season were hunting-related, whereas the only death that occurred during the LM season was caused by starvation. Intervals for each period were chosen based on the median date of the deaths for each period. We tested for differences in survival between sex and age classes using a 2-tailed t -test ($P = 0.05$).

Population Growth and Short-Term Viability

We constructed a postbreeding, 2-sex, age-classified, stochastic matrix model to estimate annual stochastic population growth (λ) and its 95% confidence interval. For environmental stochasticity in the model, we assumed that 1) environmental conditions in successive years were uncorrelated; 2) fecundity and survival rates were uncorrelated, but annual survival rates of each sex- and age-class were correlated; 3) all cougars were equally at risk within the study area (no spatial structure); 4) no catastrophes or bonanzas occurred; 5) cougars were senescent at 12 years of age (Beier 1996); and 6) male density did not affect female fecundity, with the exception that a male density of zero would cause a zero fecundity rate. Different survival rates of adult males and females during this study justified the use of a 2-sex, Leslie matrix model (Caswell 2001) composed of 24 classes (Fig. 3). Males and females of the same age succeeded each other from row to row and column to column (Caswell 2001), and subdiagonals were filled with the average demographic rates for the period 1998–2003. The dominant eigenvalue of this matrix corresponded to the finite rate of increase (λ_1) of the population, and the dominant right eigenvector to the SAD (Caswell 2001). We assessed the relative influence of each parameter r on the population growth rate by determining and comparing their elasticity (E_r), defined as

$$E_r = \frac{r}{\lambda_1} \frac{\partial \lambda_1}{\partial r}$$

(Morris and Doak 2002), where $\partial \lambda_1$ is the change in the growth rate caused by a 10% increase (∂r) in each parameter. As part of a descriptive analysis of population growth from 1998 to 2003, we examined annual survival rates in 5 distinct matrices and calculated annual dominant eigenvalues, despite having few animals represented in each sex and age category during some years.

	KitF	KitM	YeaF	YeaM	3F	3M	...	11F	11M	12F	12M
KitF	$m_{3f}S_{3f}$	0	$m_{3f}S_{3f}$	0	$m_{4f}S_{3f}$	0	...	$m_{12f}S_{11f}$	0	$m_{13f}S_{12f}$	0
KitM	$m_{3m}S_{3f}$	0	$m_{3m}S_{3f}$	0	$m_{4m}S_{3f}$	0	...	$m_{12m}S_{11f}$	0	$m_{13m}S_{12f}$	0
YeaF	S_{3f}	0	0	0	0	0	...	0	0	0	0
YeaM	0	S_{3m}	0	0	0	0	...	0	0	0	0
3F	0	0	S_{3f}	0	0	0	...	0	0	0	0
3M	0	0	0	S_{3m}	0	0	...	0	0	0	0
...
11F	0	0	0	0	0	0	...	0	0	0	0
11M	0	0	0	0	0	0	...	0	0	0	0
12F	0	0	0	0	0	0	...	S_{11f}	0	0	0
12M	0	0	0	0	0	0	...	0	S_{11m}	0	0

Figure 3. Structure of the Leslie matrix used to model population growth for female and male cougar kittens (KitF, KitM), yearlings (YeaF, YeaM), and adult (xF, xM, where x is the age class from 3 to 12) in the Pacific Northwest, USA, from 1998 to 2003. In the first 2 rows, fecundity rates (F_x) represent the probability that a female of age x will give birth to a male ($m_{xm} \times S_{(x-1)f}$) or female ($m_{xf} \times S_{(x-1)f}$) kitten. The survival rates for kittens (S_{3f} , S_{3m}), yearlings (S_{3f} , S_{3m}), adult males (S_{xm}), and adult females (S_{xf}) are the elements of the second subdiagonal.

Because we had insufficient kitten survival data during some years, we used the average kitten survival rate for all the annual matrices.

Our model took the form $\mathbf{n}(t) = \mathbf{L} \times \mathbf{n}(t - 1)$, where \mathbf{n} is the vector of population abundance, t is the time in years, and \mathbf{L} is a Leslie matrix (Fig. 3). At time zero, \mathbf{n} was the vector of initial abundance, defined by the average density, extrapolated to the entire 32,800-km² study area.

Environmental stochasticity was incorporated into our model by randomly generating the F_x and S_x elements of \mathbf{L} at every time step from normal distributions with standard deviations given in a matrix \mathbf{V} . Because there was no biological reason that variances of the average survival rates of each sex- and age-class should be different within a year and because annual sample sizes were low for some classes, we used the standard deviation of annual survival rates for all radiocollared animals combined to define environmental stochasticity in \mathbf{V} (Caswell 2001).

We included demographic stochasticity in our model by drawing the number of survivors in each sex-age class from a binomial distribution (based on the abundance $n_i(t)$ of each i th class and on the survival rates s_i from \mathbf{L}) and the number of kittens born each year from a Poisson distribution, using the random number generator of RAMAS 4.0 (Applied Biomathematics, Setauket, New York). Consistent with the youngest age reported in literature (Maehr et al. 1989, Logan and Sweanor 2001), we set age at first parturition at 1.5 years.

To obtain the stochastic growth rate λ , we projected the population 30 times over 1,000 years or until it fell to $n = 0$ animals. For every simulation, we computed the geometric mean of $[n(t + 1)]/n(t)$ over all pairs of adjacent years to obtain a first estimate of λ (Morris and Doak 2002). We selected the arithmetic mean and 95% confidence intervals of all simulations as the best estimate of the population growth rate.

We assessed population viability by examining the population trajectories of 5,000 simulations of our model projected over 25 years. Initial abundance was set by our density estimates

extrapolated to the 32,800-km² MCP area. All PVAs were performed with the software RAMAS.

Results

Trends in Minimum Density and Abundance

We captured and monitored 52 cougars between 14 December 1998 and 20 May 2003, resulting in 19,337 cougar-radio-days and 2,737 radio-locations. Twenty were males (8 adults and 12 yearlings), and 32 were females (27 adults and 5 yearlings). The MCP of all cougar locations in this study encompassed approximately 32,800 km² (48°21'N–49°35'N, 115°57'W–119°04'W), whereas the 95% adaptive-kernel composite estimate for all animals was 5,600 km² (Fig. 1). Home ranges of adult females represented by >30 locations ($n = 18$ females, $\bar{x} = 112$ locations) averaged 653 km² but were highly variable (95% CI = 1,671). Annual density estimates and trends from the annual count of monitored cougars in each class were very similar to the estimates based on SAD multiplied by the adult female density, although SAD estimates were slightly higher when yearlings and kittens were included (Fig. 4). Average annual minimum density varied from a high of 1.46 cougars/100 km² in 1998–1999 to 0.85 cougars/100 km² in 2002–2003, with an average annual change of $-12 \pm 16\%$ (mean \pm 95% CI; Table 1). The average minimum density for all years was 0.46 ± 0.24 adults/100 km² and 1.09 ± 0.54 cougars/100 km². Total abundance in the 32,800-km² study area was estimated at 357 cougars (1.09 cougars/100 km²), which was used as the starting point of every PVA.

Fecundity

Based on observations of 15 litters, we estimated mean litter size at 2.53 ± 1.01 . The M:F ratio of 1:1.13 for 17 kittens was not different from equality ($Z = 0.25$, $P = 0.81$). We documented only 1 successful interbirth interval (18 months) but used this value in our model because it was consistent with results from studies with larger sample sizes over longer time series (19.7 months, Ross and Jalkotzy 1992; 17.3 months, Lopez-Gonzalez 1999; 17.4 months, Logan and Sweanor 2001). Further, we estimated that 75% of all

adult females were reproductively successful (pregnant or with offspring) in any year. This approximation could overestimate fecundity, considering the 41–64% range reported by Robinette et al. (1961), Towell et al. (1984, 1988), and Ross and Jalkotzy (1992), but seemed reasonable to us because highly exploited populations often exhibit higher productivity than populations at carrying capacity (Ricklefs 1990). Based on these parameters, we estimated the maternity rate to be 0.63 kittens of each sex per year ($[2.53 \times 0.5 \times 0.75]/1.5$) for females older than 2, and 0.32 for females between 1 and 2 (half the adult rate because females can start to reproduce at 1.5 yr old).

Survival

Hunting accounted for 22 of the 24 deaths of radiocollared cougars, and indirectly caused the death of 5 of 21 dependent kittens by death of the mother. We censored 9 of the 52 monitored cougars after they lost their collars or moved out of the study area. We included their radio-days in the survival analysis until censoring, but excluded them thereafter. Four other cougars were excluded from all analyses because 1 died as a result of capture procedures and 3 others lost their radiocollars or could not be found in the study area after day 1. Overall, 31 of the 52 radiocollared cougars lived or were monitored for less than 1 year after capture. The average annual survival rate for all radiocollared cougars from 1998 to 2003 was $59 \pm 20\%$, but variation occurred between age and sex classes, and among years (Table 2). Average survival rate was higher for adult females (77%) than for adult males (33%, $t = 7.80$, $df = 34$, $P < 0.01$) or yearlings (34% $t = 10.33$, $df = 43$, $P < 0.01$). Survival did not differ between yearling males (37%) and yearling females (32%, $t = 0.35$, $df = 15$, $P = 0.73$), so they were pooled. Yearling survival (34%) was lower than kitten survival (57%, $t = 4.92$, $df = 36$, $P < 0.01$), so we kept the 2 estimates distinct in our model. In total, we recorded only 2 natural mortalities for radiocollared cougars: 1 adult female was found with a broken neck and 1 adult male starved. The standard deviation of the annual survival rates of all radiocollared cougars was 0.17, which was used in the matrix V to incorporate environmental stochasticity in our PVA model.

Population Growth and Short-Term Viability

The deterministic finite rate of increase λ_1 of the average projection matrix was 0.87. The SAD was 30% adult females, 8% adult males, 25% yearlings (1:1 sex ratio), and 37% kittens (1:1 sex ratio). There were very few animals (particularly males) in older age classes (Fig. 5), and animals 4 years of age and older represented only 22% of the population. Annual deterministic growth rates followed the pattern of adult female survival rates (Fig. 6), starting with $\lambda_1 = 1.24$ in 1998 and then progressively declining to 1.04, 0.92, 0.59, and 0.87 in 2002–2003. Elasticity analysis confirmed that adult female survival affected growth rate the most, with $E_f = 0.69$, whereas the elasticity value was 0 for adult males, 0.17 for yearling survival, 0.17 for kitten survival, and 0.19 for maternity rate (elasticities do not sum to 1 because both maternity and female survival rates were involved in fecundity rates [$F_x = m_{x+1} \times S_{xf}$]).

The stochastic finite rate of population growth was $\lambda = 0.80 \pm 0.11$. On average, the population fell to half its original size after 5 years and had less than 30 animals after 25 years (Fig. 7).

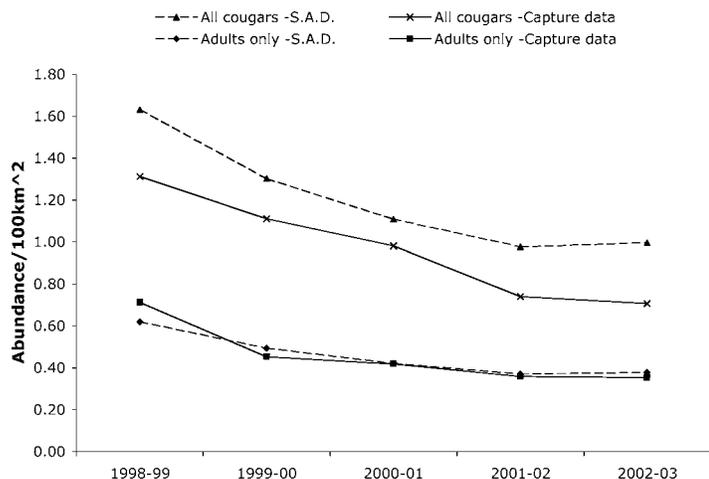


Figure 4. Adult and total cougar density in the Pacific Northwest USA, from 1998 to 2003, calculated with the 95% adaptive-kernel composite home range method for adult females and projected with both capture data and stable age distribution (SAD) vector to calculate adult male and yearling densities. Kitten density was calculated with the SAD.

Table 1. Adult and total cougar minimum density (per 100 km²) in the Pacific Northwest, USA, as determined by the 95% adaptive-kernel composite home ranges of adult females (km²) and the abundance (*n*) of kittens, yearlings, and adult females and males in the study area, 1998 to 2003.

	Composite home range (km ²)	Kitten		Yearling		Adult F	Adult M		Density	
		SAD ^a	SAD ^a	Cap. ^b	Cap. ^b	Cap. ^b	SAD ^a	Cap. ^b	Adult	Total
1998–1999	1,826	11.1	7.3	2	9	2.3	4	0.67	1.47	
1999–2000	3,308	16.1	10.6	8	13	3.3	2	0.47	1.21	
2000–2001	3,582	14.9	9.8	7	12	3.1	3	0.42	1.05	
2001–2002	4,744	17.3	11.4	5	14	3.6	3	0.36	0.86	
2002–2003	5,641	21.1	13.8	5	17	4.4	3	0.37	0.85	
Average	3,820	16.1	10.6	5.4	13	3.3	3	0.46	1.09	

^a Abundance estimated with the stable age distribution (SAD).

^b Number of captured (Cap.) and monitored animals in the study area.

Discussion

Trends in Minimum Density and Abundance

We documented dispersal of collared cougars in and out of the core study area but did not have enough cougars in all jurisdictions to allow comparison between these groups. Therefore, we assumed that density and demographic rates were similar for cougars in Washington, USA; Idaho, USA; and British Columbia, Canada. Trends in minimum relative density corresponded to trends in population demography and growth rate, adding corroborative evidence to the estimated demographic decline. Average minimum adult and total population densities were in the lower range of densities reported for cougars elsewhere (from 0.44 to 13.03 cougars/100 km², Smallwood 1997). Our estimates were comparable to densities observed in 2 populations in Utah, USA (0.37 adults/100 km², Lindzey et al. 1994; 0.96 cougars/100 km², Lopez-Gonzalez 1999), but considerably lower than those observed in 5 other populations, including Alberta, Canada (2.7 to 4.2 cougars/100 km², Ross and Jakoltzy 1992); British Columbia, Canada (3.5 to 3.7 cougars/100 km², Spreadbury et al. 1996); Idaho, USA (2.9 adults/100 km², Hornocker 1970); and New Mexico, USA (1.72 to 3.91 cougars/100 km², Logan and Sweanor 2001). Even the starting density, at 1.47 cougars/100 km² in 1998–1999, was lower than most other populations, suggesting that the popular perception that cougars were at an extremely high density was incorrect.

Although intense trapping efforts were repeated each winter, our estimates should be considered minimums because capture efforts were not distributed evenly in the study area. We strongly suspect the existence of uncaptured individuals in the annual 95% adaptive-kernel home range of the adult females. Higher SAD estimates for total density might indicate we did not capture and monitor all yearlings in the study area, but it could also mean the population structure has not reached stability yet. The gradual

annual increase in the composite home range area as new animals were added to the study may also have contributed to the estimated decline in density (Smallwood 1997). However, captured animals, especially males, leaving the composite range likely offset uncaptured animals in the 95% composite female home range. Further, our estimates included animals that were monitored for only a few days. Other cougar studies probably suffered from the same problem of uncaptured animals and lack of population closure, so our density estimates, although minimums, should be comparable to others in the literature. We caution readers not to interpret our density estimates as absolute real numbers because of the uncertainties involved but to interpret them as relative trend indicators and as corroborative evidence of the demographic trends.

Demographic Rates

Litter size (2.53) was consistent with those reported elsewhere (2.4, Hemker et al. 1986; 2.2, Ross and Jakoltzy 1992; 2.4, Lindzey et al. 1994; 3, Logan and Sweanor 2001). However, small sample size made it necessary to estimate interbirth interval, age at first litter, and proportion of successful reproducing females from the literature. Because the elasticity value of maternity rate was relatively low (0.19), uncertainties in fecundity values should have a negligible influence on population projection results.

Survival rates indicated that this cougar population was heavily hunted (causing 92% of radiocollared cougar mortality) compared with other populations (15%, Logan et al. 1986; 5%, Logan and Sweanor 2001; 35%, Spencer et al. 2001). The overall survival rate (0.58) was similar to that encountered in Arizona (0.62, Cunningham et al. 2001). Survival rate of adult females (0.77) was similar to those of other cougar populations (0.77, Lopez-Gonzalez 1999; 0.82, Logan and Sweanor 2001; 0.77 for all adults, Spencer et al. 2001) and higher than the 0.67 reported by Cunningham et al. (2001). However, adult male survival (0.33)

Table 2. Annual survival rates (% [*n*]) for cougar kittens (0–1 yr), yearlings (1–2 yr), and adult (2–12 yr) males and females in the Pacific Northwest, USA, from 1998 to 2003.

	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003	Mean	SD
Kittens	—	25 (4)	100 (3)	75 (8)	43 (7)	57 (21)	11
Yearlings	100 (2)	53 (7)	24 (7)	17 (5)	41 (5)	34 (17)	18
Adult males	21 (3)	50 (2)	27 (3)	26 (3)	100 (3)	33 (8)	24
Adult females	100 (9)	90 (12)	91 (11)	52 (13)	76 (16)	77 (28)	10
Total^a	69 (14)	76 (21)	65 (20)	35 (22)	77 (23)	59 (52)	10

^a Includes only radiocollared cougars.

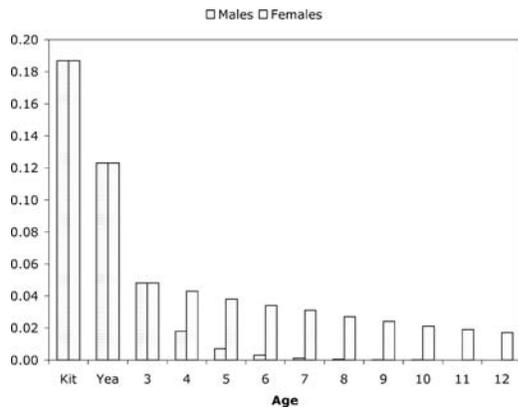


Figure 5. Stable age distribution of the cougars in the Pacific Northwest, USA, based on survival and fecundity rates estimated in the study area from 1998 to 2003.

was much lower than in other areas (0.62, Lopez-Gonzalez 1999; 0.58, Cunningham et al. 2001; 0.91, Logan and Sweanor 2001). Similarly, kitten and yearling survival were lower than most rates reported in the literature. However, tracking involved uncertainties because of the possibility of unseen but live kittens, so kitten survival could have been underestimated. Still, our estimate (0.57) was in the range reported by other studies (0.72, Hemker et al. 1986; 0.59 to 0.63, Logan and Sweanor 2001; 0.42, Lopez-Gonzalez 1999; 0.76, Robinette 1961). Yearling survival (0.34) was lower than reported elsewhere (0.56 and 0.88 for subadult males and females, Logan and Sweanor 2001; 0.60 and 0.80 for juvenile males and females, Spencer et al. 2001).

The elasticity of adult female survival outweighed that of any other parameter, highlighting the large influence of adult female survival on population growth and reducing the effect of uncertainties from other parameters that had smaller sample sizes and larger standard deviations.

Population Growth and Viability

The estimated declining trend in minimum annual density ($-12 \pm 16\%$) corresponded to the decline indicated by the stochastic ($-20 \pm 11\%$) and deterministic (-13%) growth rates, adding corroborative evidence for the decline. Because the stochastic growth rate incorporates environmental and demographic variability, it is believed to be more realistic than the deterministic growth rate (Caswell 2001, Morris and Doak 2002). The

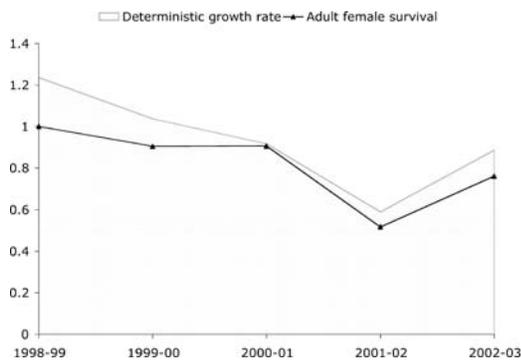


Figure 6. Annual survival rates of adult females and deterministic growth rates λ_1 (dominant eigenvalue of annual matrix model) for cougars in the Pacific Northwest, USA, 1998 to 2003.

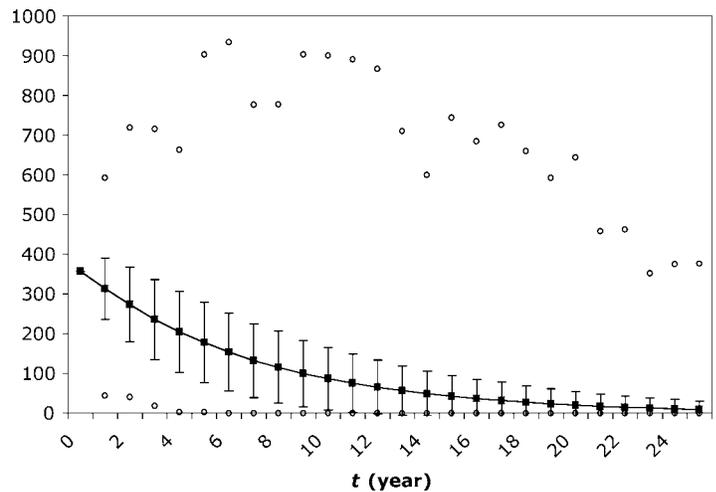


Figure 7. Simulated trajectory of the cougar population in the Pacific Northwest, USA, based on survival and fecundity rates from 1998 to 2003. Squares represent the annual average abundances, vertical lines are standard deviations, and empty circles are the maximum and minimum values obtained in 5,000 simulations.

difference between the 2 values in our model ($\Delta\lambda = 0.07$) is probably related to the large magnitude of environmental variation in demographic rates ($SD = 0.17$), which could have been reduced by larger sample sizes. Regardless of which method was used, both indicated a steeply declining population.

Our results are limited by uncertainties in some of the model parameters and density estimates. However, the very high elasticity value for adult female survival (0.69) and relatively large sample size ($n = 28$) for this parameter seem to support the population decline we report, despite uncertainties in other parameters. They also indicate that a small increase in female survival would suffice to increase λ . Regarding our density estimates, the simulated population trajectories would simply have taken longer to reach extirpation if they had been higher, but the growth rate would not have been affected.

A limitation for population projections is the underlying model assumptions that all means and standard deviations for demographic rates will remain constant in space and time. This is unlikely to happen, especially because this population is managed under 3 jurisdictions that have different cougar-management regimes. Therefore, long-term projections should be interpreted

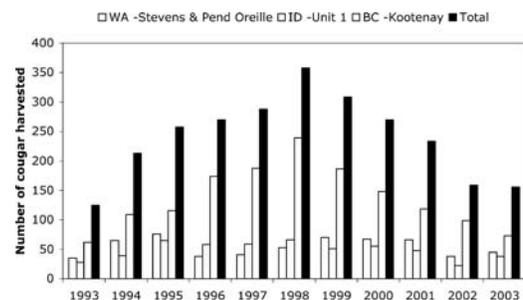


Figure 8. Number of cougar harvested in the surrounding management units of our study area, from 1993 to 2003 (D. Martorello, Washington Department of Fish and Wildlife, unpublished data; W. Wakkinen, Idaho Fish and Game, unpublished data; G. Woods, British Columbia Ministry of Water Land and Air Protection, unpublished data).

with caution. Further, immigration from neighboring populations could increase the viability of this population (Beier 1993, Sweanor et al. 2000), or a very sparse cougar density could trigger a lower hunting effort and/or success. In our case, the lack of population closure and extracomposite movements of some cougars suggest this population is part of a larger metapopulation. Additional research should be made to determine demographic rates of the cougars surrounding our study area and to verify whether this population is a sink for adjacent populations. Nevertheless, the number of cougars harvested in management units adjacent to our study area declined from 1998 to 2003 (Fig. 8), which might indicate decreasing cougar abundance and add corroborative evidence to the population decline.

Our results reject the hypothesis that cougars are currently increasing in northeastern Washington, USA; southern British Columbia, Canada; and northern Idaho, USA. The cougar population appears to be declining. This decline could be reversed if harvest rates were decreased, especially for adult females. The increased level of cougar complaints following 1996 does not seem to be due to excessively high densities and growth rates but could be related to 1) very young age structure of the population caused by heavy hunting (Fig. 5); 2) increased human intrusion into cougar habitat; 3) low level of social acceptance of cougars in the area; or 4) habituation of cougars to humans. Further studies are needed to elucidate these possible factors. Educational programs, such as the one undertaken in western Washington, USA (Project C.A.T.; Koehler and Nelson 2003) and strategies to haze cougars away from humans might help alleviate the social tension related to cougars.

Management Implications

Our research indicates that wildlife managers should not assume that increasing cougar/human complaints correspond with increasing cougar populations. Indeed, increased complaints may accompany a rapidly declining population as shown here. Furthermore, increased hunting could actually result in increased

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cougar complaints because of the younger age structure of the cougar population and the higher proclivity of young animals to encounter humans and cause complaints. Sustainable hunting regulations and bag limits should not be based on numbers of cougar complaints—but should be based on estimated demographic trends obtained through census or radiotelemetry.

Assuming the precautionary principle (Cooney 2004), we recommend that cougar managers in the Pacific Northwest 1) reduce the exploitation of this population to a more conservative, sustainable level, especially for adult females; 2) keep monitoring this and other populations to assess trends in cougar population demography and cougar complaints; and 3) collaborate in conservation and monitoring efforts with wildlife managers from adjacent states or provinces where cougar populations overlap.

The conflicts surrounding cougar management in our study area are not uncommon in other regions of North America. Other populations that are believed to be increasing, as suggested by more frequent cougar complaints, could be declining as well. Conducting similar demographic analyses where complaints are increasing could shed light on this situation.

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