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In My Opinion

Research to Regulation: Cougar Social Behavior as a Guide for Management

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ABSTRACT Cougar (*Puma concolor*) populations are a challenge to estimate because of low densities and the difficulty marking and monitoring individuals. As a result, their management is often based on imperfect data. Current strategies rely on a source–sink concept, which tends to result in spatially clumped harvest within management zones that are typically approximately 10,000 km^2. Agencies often implement quotas within these zones and designate management objectives to reduce or maintain cougar populations. We propose an approach for cougar management founded on their behavior and social organization, designed to maintain an older age structure that should promote population stability. To achieve these objectives, hunter harvest would be administered within zones approximately 1,000 km^2 in size to distribute harvest more evenly across the landscape. We also propose replacing the term “quota” with “harvest threshold” because quotas often connote a harvest target or goal rather than a threshold not to exceed. In Washington, USA, where the source–sink concept is implemented, research shows that high harvest rates may not accomplish the intended population reduction objectives due to immigration, resulting in an altered population age structure and social organization. We recommend a harvest strategy based on a population growth rate of 14% and a resident adult density of 1.7 cougars/100 km^2 that represent probable average values for western populations of cougars. Our proposal offers managers an opportunity to preserve behavioral and demographic attributes of cougar populations, provide recreational harvest, and accomplish a variety of management objectives. We believe this science-based approach to cougar management is easy to implement, incurs few if any added costs, satisfies agency and stakeholder interests, assures professional credibility, and may be applied throughout their range in western North America. © 2013 The Wildlife Society.

KEY WORDS cougar, harvest management, harvest quota, intrinsic growth rate, management zone, *Puma concolor*, regulation, social structure, source–sink, Washington.

The history of cougar (*Puma concolor*) management in Washington and for the western United States as a whole has been dominated by political and special interest agendas creating a challenge for wildlife managers (Kertson 2005, Beausoleil and Martorello 2008, Mattson and Clark 2010, Jenks 2011, Peek et al. 2012). This is magnified by the lack of reliable information on cougar population size, density, and outcomes of management strategies (Cougar Management Guidelines Working Group 2005). In recent decades, satellite and Global Positioning System telemetry and long-term field investigations in 6 different areas in Washington (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2008, 2009*a*, *b*; Maletzke 2010; Kertson et al. 2011*a*, *b*; R. A. Beausoleil, unpublished data), and throughout the West (Logan and Sweanor 2001, Cougar Management Guidelines Working Group 2005, Stoner et al. 2006, Hornocker and Negri 2010, Robinson and DeSimone 2011) have elucidated cougar ecology, providing managers a new scientific basis to help guide management.

Behavior and social organization are important aspects of many species' biology and should be considered for management, particularly for low-density territorial carnivores occupying the apex of the trophic hierarchy (Wielgus and Bunnell 1994, Caro et al. 2009, Packer et al. 2009, Treves 2009, Estes et al. 2011). Maintaining mature cougars is important because they influence rates of immigration and emigration, spatial distribution, reproduction, and kitten survival (Cougar Management Guidelines Working Group 2005, Hornocker and Negri 2010; Cooley et al. 2009*a*, *b*).

We propose a science-based approach to regulated harvest management founded on cougar behavior and social organization, in which harvest is regulated to maintain an older age structure to promote population and social stability. This model for cougar management addresses concerns of various constituencies to 1) provide a sustainable harvest, 2) provide quality recreational experience to the hunting public, 3) maintain viable cougar populations, and 4) more explicitly

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recognize the values of the non-consumptive public by maintaining the behavioral integrity of cougar populations.

We base our recommendations on research from Washington demonstrating that a high harvest rate may not accomplish local population reductions and may result in altering the age structure and social organization of the population. This may have unplanned consequences for cougar–prey dynamics and cougar–human conflict (Knopff et al. 2010, White et al. 2011, Kertson et al. 2013). More than US$ 5 million and >13 years (1998–2011) have been invested in cougar research in Washington at 6 study sites across a diverse landscape (Fig. 1). We distill findings from these investigations and propose strategies to help managers navigate the myriad of agendas that encompass carnivore management for a more predictable management outcome, especially in the unpredictable atmosphere of politics and advocacy. Our objective for this review is to provide a data-driven management system that can be applied consistently among management units that incorporates both species behavior and human interests.

CURRENT COUGAR MANAGEMENT STRATEGIES

Management agencies throughout the west use a variety of strategies and techniques to regulate cougar harvest, including general-season hunts with no harvest limit or season restrictions, limiting the number of hunters through permits, and limiting harvest through quotas or bag limits. The use of trailing hounds to hunt cougars is permitted in the majority of states and provinces (Beausoleil et al. 2008). In this manuscript, we propose replacing the term "quota" with "harvest threshold" because quotas often connote a harvest target or goal rather than a threshold not to exceed, and we propose that harvest should not exceed the intrinsic rate of population growth.

Current management strategies rely on a source–sink concept (Laundré and Clark 2003) and are administered within cougar management zones (CMZs), that are typically about 10,000 km^2 and often have management objectives to reduce or maintain cougar populations (Logan and Sweanor 2001). However, dispersal by cougars from adjacent areas may thwart efforts to locally reduce cougar populations (Lambert et al. 2006, Robinson et al. 2008; Cooley et al. 2009*a*). Conversely, where managers want to maintain cougar populations and apply harvest thresholds to zones, harvest may still be locally excessive when CMZs are >1,000 km^2 and the majority of the harvest occurs in clusters where hunter accessibility is relatively great (Ross et al. 1996). Although local population sinks may be re-populated by immigration of subadults, disruption may occur to the intrinsic social and spatial organization of the population, which may result in a demographic composition dominated by subadults (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2009*b*). This situation may create unanticipated consequences, including an increase in the use of residential areas by cougars and in human–cougar complaints (Maletzke 2010, Kertson et al. 2011*b*).

HISTORY OF COUGAR MANAGEMENT IN WASHINGTON

Cougar management in Washington began in 1966 when their status changed from a bounty animal to a big-game species with hunting seasons and harvest limits (Washington

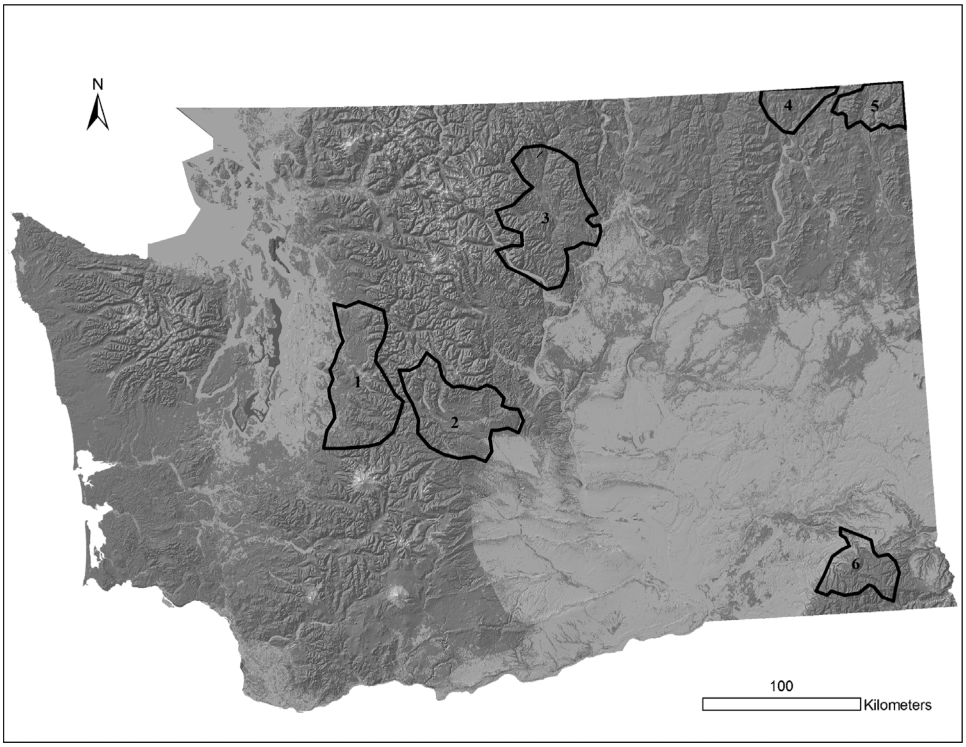

Figure 1. Six cougar research areas in Washington, USA, 2001–2012: (1) western WA; (2) central WA; (3) north-central WA; (4 and 5) northeast WA; (6) southeast WA.

Department of Fish and Wildlife [WDFW] 2008). This change came with a series of regulations, including mandatory reporting (1970), inspection and sealing of cougar pelts for demographic data (1979), and submitting a tooth from harvested animals for age analysis (mid-1980s). From 1980 to 1995, cougar harvest seasons remained static with a 6–8-week season.

Politics began to direct cougar management in 1996 when Washington voters approved Initiative 655 (I-655). Initiative 655 banned the use of dogs for hunting cougar and has been pivotal in framing the debate over cougar management in Washington since then (Kertson 2005, Beausoleil and Martorello 2008). With the use of dogs banned and anticipated decrease in cougar harvest, WDFW 1) replaced limited permit-only seasons with general seasons, 2) increased season length from 7.5 weeks to 7.5 months, 3) increased bag limits from 1 to 2 cougar/year, and 4) decreased the price of transport tags from US$ 24 to $ 5. The response to these changes resulted in increased tag sales from an annual average of 1,000 prior to I-655 to approximately 59,000/year since 1996, and this action increased harvest from an average of 121 (SD = 54, 1980–1995) to an average of 160 (SD = 44, 1996–2011)/year. Hunting opportunities and harvest were not evenly distributed, primarily increasing in areas where social tolerance for cougars was low, deer hunter density was high, and human access was high; during this time, cougar densities were unknown but assumed to be increasing (Jenks 2011, Lambert et al. 2006).

Since I-655 was approved, 16 legislative bills addressing cougar management have been introduced into the Washington legislature (http://apps.leg.wa.gov/billinfo). In 2000, Washington instituted a management concept to reduce cougar numbers in areas where complaints were high (Engrossed Substitute Senate Bill 5001-ESSB 5001). This bill and 3 others since 2003 (Substitute Senate Bill 6118-SSB 6118, Engrossed Substitute House Bill 2438-HB 2438, and Engrossed Substitute House Bill 1756-HB 1756) permitted the use of dogs in 6 counties, effectively overturning I-655 in many areas throughout Washington. In 2011, House Bill 1124 was introduced to continue hunting with hounds but failed to pass, and since the use of dogs has been prohibited statewide. However, ESSB 5001 allows the WDFW to authorize a hunt with the use of dogs when reports of conflicts with humans or their livestock exceed the previous 3-year running average.

In the midst of the political activity between 1996 and 2010, which included legislative mandates, WDFW began integrating insights from harvest monitoring (Martorello and Beausoleil 2003), and research projects (Robinson et al. 2008; Lambert et al. 2006; Cooley et al. 2009*a*, *b*; Kertson 2010; Maletzke 2010). In 2003, harvest thresholds in conjunction with a 24-hour hunter reporting hotline allowed for prompt closure of zones where the use of dogs was permitted. In 2009, the WDFW reduced the bag limit to 1 cougar/hunter/year, shortened season length to avoid some overlap with deer and elk seasons, and restricted harvest with female- and total-harvest thresholds. In 2011, WDFW managers and researchers compiled research findings and began drafting a new management strategy, an aspect of which was publicly reviewed and ultimately adopted by the Washington Fish and Wildlife Commission in spring 2012. Here, we present a synthesis of this research and develop these concepts into a management strategy.

COUGAR ABUNDANCE AND DENSITY: BEHAVIORAL CONSIDERATIONS

Estimating cougar abundance and density, as with most species, represents one of the most challenging aspects of their management. Currently, reliable estimation of cougar abundance requires expensive, field-intensive, long-term research (Hornocker and Negri 2010). Consequently, agencies use numbers of cougar complaints, cougar–human conflicts, and harvest as proxies for population size and trend (Martorello et al. 2006). However, cougar complaint reports can be unreliable (Kertson et al. 2013), and it has been shown that increasing numbers of complaints and increasing predation on mule deer (*Odocoileus hemionus*), and endangered mountain caribou (*Rangifer tarandus caribou*) in a large (10,000-km^2) heavily hunted CMZ in the Selkirk Mountains Ecosystem in northeastern Washington, northern Idaho, and southern British Columbia did not correspond to increasing densities of cougars (Katnik 2002, Robinson et al. 2002, Lambert et al. 2006). Thus, the indirect proxies of population size appeared to be plausible but were inaccurate in that heavily hunted CMZ that had approximately 38% annual removal rate of cougars.

Subsequent research in Washington was designed to examine the previous hypothesis (Lambert et al. 2006) of no direct positive correlation between harvest numbers and complaints and population densities of cougars. Working in the heavily hunted (24% of population harvested/yr), area of Kettle Falls in northern Washington, a declining female cougar population was documented as the male segment increased due to compensatory juvenile male immigration (Robinson et al. 2008). In another study area in central Washington, (Cle Elum), an opposite scenario was confirmed in that relatively low hunting mortality (11%/yr) resulted in a net emigration of younger males (Cooley et al. 2009*a*). In all cases, the population densities were remarkably similar, ranging from 1.5 to 1.7 adult (>2-yr-old), cougars/100 km^2 with total densities of about 3.5 cougars/100 km^2, including kittens and subadults. Details on estimating population densities and immigration–emigration rates have been described (Robinson et al. 2008; Cooley et al. 2009*a*, *b*; Robinson and DeSimone 2011). Additional research on 2 other study areas in western and north-central Washington showed an average resident adult density of about 1.6/100 km^2 and a total density of about 3.4/100 km^2 (R. A. Beausoleil and B. N. Kertson, unpublished data). In 3 separate study areas in Washington and Montana, increased hunting (11–38% population harvest rates) did not result in compensatory increases in cub production, cub survival, or adult survival (Robinson et al. 2008; Cooley et al. 2009*a*, *b*; Robinson and DeSimone 2011). However, variation in hunting mortality did result in compensatory immigration–emigration by primarily young males, with no net differences in total cougar numbers. Such compensatory immigration has been observed in many other highly mobile species as well (Beecham and Rohlman 1994, Merrill et al. 2006, Turgeon and Kramer 2012, Mills 2013). Therefore, increased hunting may not always result in reduced local densities of cougars, but not due to traditional density-dependent effects such as compensatory reproduction and survival; instead, increased hunting may result in compensatory immigration by mainly young males (Cooley et al. 2009*b*).

Presenting and comparing density estimates between studies is challenging because standardization is lacking (Quigley and Hornocker 2010). For example, whereas total density could temporarily fluctuate in response to immigration and emigration of subadults, density of resident breeding adults tends toward stability over time. Density estimates can also be misinterpreted from incomplete data due to differences in seasonal spatial use patterns where individuals concentrate on low-elevation ungulate winter ranges, often comprising only a portion of the population's annual distribution (Maletzke 2010). When annual boundaries of individual cougar territories are unknown, density estimates may result in inflated values and substantial overestimation of population size (Maletzke 2010). However, there is remarkable consistency in the western United States and Canada where long-term research has been conducted; resident adult densities average 1.6 cougar/100 km^2, while total densities including kittens and subadults average 2.6 cougar/100 km^2 (Quigley and Hornocker 2010). Our research in Washington corroborates these findings because adult densities averaged 1.7/100 km^2 (Cooley et al. 2009*b*; R. A. Beausoleil and B. N. Kertson, unpublished data). Therefore we encourage a more explicit, standardized approach of using estimates of adult densities for population management objectives and caution against using total densities, because they do not provide for reliable estimation of population parameters and harvest impacts (Robinson et al. 2008; Cooley et al. 2009*b*).

In Washington, where prey biomass was consistent and cougar harvest ranged from 11% to 38% of the cougar population per year, the age structure, survival, sex ratio, reproductive rate, and spatial use patterns of cougars differed (Lambert et al. 2006; Cooley et al. 2009*b*; Maletzke 2010). Where annual harvest was 24%, mean age at harvest was 27 months compared with 38 months where annual harvest was 11%. In addition, in areas of greater relative harvest, male home-range sizes were larger (753 km^2 vs. 348 km^2), and home-range overlap between males was greater (41% vs. 17%). Cougars, especially males, evolved with a social dynamic to patrol and defend a territory regardless of whether their home-range size is determined by prey density or social tolerance (Hornocker 1969, Pierce et al. 2000, Logan and Sweanor 2010). As adult mortality increases, territorial boundaries diminish. Immigrating subadults may establish home ranges readily, and their home ranges may overlap significantly, which may influence rates of predation and the distribution of prey and potentially increase probabilities for interactions with humans (K. A. Peebles, Washington State University, unpublished data).

The social system and territoriality observed for cougars is similar among many species of solitary felids, although it may manifest itself differently for males and females (Sunquist and Sunquist 2002). Although the role of social ecology for cougars will continue to be debated in the future, it is important to acknowledge that harvest intensity can affect spatial use patterns of cougars as well as their population demographics, as demonstrated for other hunted carnivore populations (Packer et al. 2009).

HARVEST MORTALITY VERSUS TOTAL MORTALITY

Although knowledge of population abundance and density is critical for sound management of cougars, it is also important that managers be aware that harvest mortality can be additive to natural mortality (Robinson et al. 2008; Cooley et al. 2009*b*; Robinson and DeSimone 2011). Failing to account for and include all mortality sources may obscure estimates of population trajectory and underestimate the impact of harvest on demographics and cougar social structure (Cooley et al. 2009*b*; Morrison 2010; Robinson and DeSimone 2011). Unfortunately, reliable knowledge of non-harvest mortality is difficult to quantify (Cougar Management Guidelines Working Group 2005), because harvest may not necessarily be representative of age structure of the population (R. A. Beausoleil, B. N. Kertson, and G. M. Koehler, unpublished data).

To illustrate the importance of considering non-harvest mortality, we documented 79 mortalities of radiomarked cougars during 4 concurrent research efforts in Washington. Of these, 49% were non-hunter harvest mortalities; 14% from agency control, 6% from intraspecific strife, 6% due to motor-vehicle collisions, 4% from disease, 4% attributed to Native American predator-control efforts, 3% due to injuries sustained during pursuit of prey, 3% from poaching or illegal harvest, and 10% from undetermined sources. In the western Washington study area, hunter harvest mortality averaged $\leq$2 animals/year from 2003 to 2008 and annual survival rate of the study population was 55% ($SD = 7.8$, $n = 5$ yr; B. N. Kertson, unpublished data). A significant mortality factor for this population was from feline leukemia virus exposure along the wildland–urban interface, resulting in an observed average annual survival rate of 55%, less than that for a heavily hunted population in Washington with 79% annual survivorship (Cooley et al. 2009*b*). These examples demonstrate the importance that non-harvest mortality can have in cougar population dynamics.

POPULATION GROWTH AND MAXIMUM SUSTAINED YIELD

The growth rate for an unhunted population, or intrinsic rate of population growth, can be described as the rate we expect the population to grow if it did not experience additive hunting mortality. Because kitten mortality and non-harvest mortality can be additive to hunting mortality, we calculated the intrinsic growth rate by censoring all harvest mortalities. In Washington, the unhunted growth rate was 1.14 ($SD = \pm 0.023$) for 3 different populations (Selkirk Mountains, Kettle Falls, and Cle Elum; Morrison 2010). The intrinsic growth rate in northwest Montana was estimated by removing hunting that resulted in a population growth rate of 1.15–1.17 (Robinson and DeSimone 2011). Although growth rate may be considered equivalent to the maximum sustainable yield, the rate of growth for an unhunted population should not be the goal for harvest but rather a maximum not to exceed if a stable population is to be achieved. Using maximum sustainable yield as a management target has been cautioned against, because it does not incorporate the uncertainty of stochastic events on population abundance and may present a potential for over-harvest (Caughley and Sinclair 1994). Setting adult harvest limits to the intrinsic rate of growth of 14% should help to balance immigration and emigration among harvest units and result in greater stability of cougar densities and age structure.

HARVEST UNITS AND HARVEST THRESHOLDS

Cougars are often managed in administrative zones (Logan and Sweanor 2001), which represent an amalgam of smaller Game Management Units (GMUs). Commonly these CMZs are designated as population "sources" and "sinks" where management objectives are to maintain or decrease population levels, respectively (Laundré and Clark 2003). In Washington, 139 GMUs are partitioned throughout the state and are used to manage harvest and habitat for a variety of game species (Fig. 2). In 2011, these GMUs were combined into 13 CMZs, each comprised from 3 to 22 GMUs and encompassing 1,873–14,947 km^2 of forested and shrub-steppe habitat (total = 90,783 km^2; Fig. 3). Five CMZs had a harvest limit of 6–20 cougars, and 8 did not have limits. Individual GMUs with high hunter access and suitable snow conditions accounted for 25–50% of the total harvest within the CMZs, which has been repeated over multiple years (WDFW 2011). This uneven distribution of harvest, or harvest clustering, may create local population sinks in areas within CMZs designated as sources and may disrupt the social organization of cougars as previously explained. Additionally, this uneven distribution of harvest may result in some GMUs with little or no harvest, creating angst among hunters who feel harvest opportunity was inequitable.

Setting harvest thresholds can help to distribute harvest, minimize risk of overharvest (Ross et al. 1996), and help maintain recreational opportunity and quality of hunter experience. However, it is important to note that harvest thresholds may become less effective for distributing harvest as CMZ size increases, and harvest may be concentrated within areas where access is high (i.e., harvest clustering). Harvest thresholds to limit harvest may be more effective where harvest is distributed evenly among GMUs rather than applied to the larger CMZs. Where GMUs are small, habitat is limited, or a quota of ≤ 1 cougar is allocated, combining adjacent GMUs to reach a size of approximately 1,000 km^2 may be recommended.

HUNTER CONSIDERATIONS

Age and sex of harvest can be an important factor influencing population dynamics of big-game species. Unlike ungulates

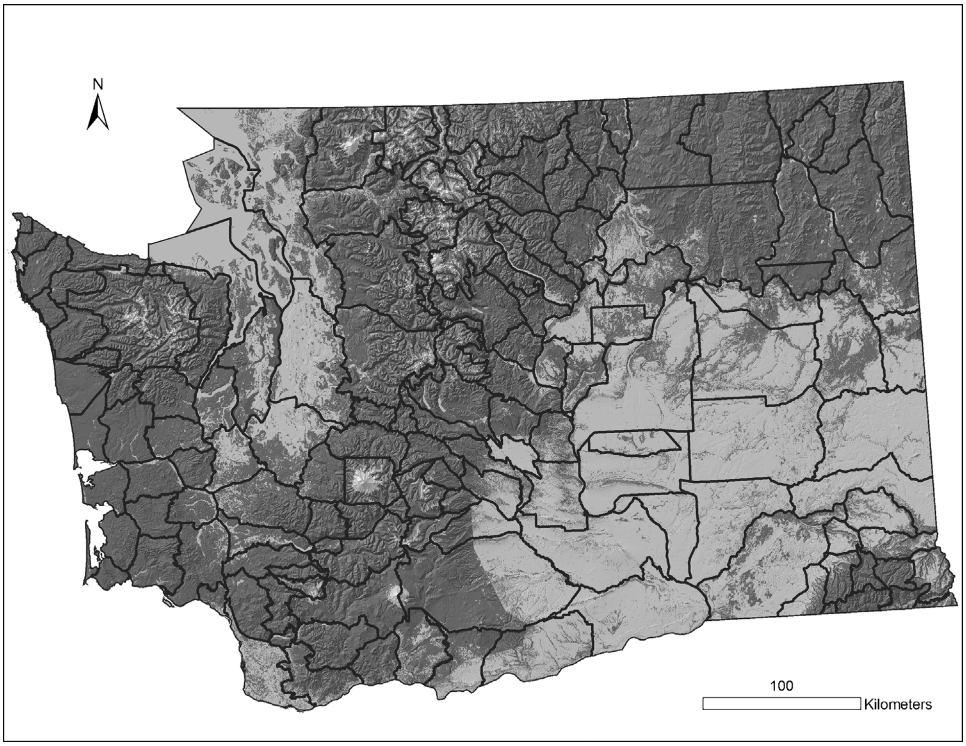

Figure 2. Distribution of cougar habitat (shaded dark) and current game-management units (outlined in black) in Washington, USA, Washington Department of Fish and Wildlife, 2012.

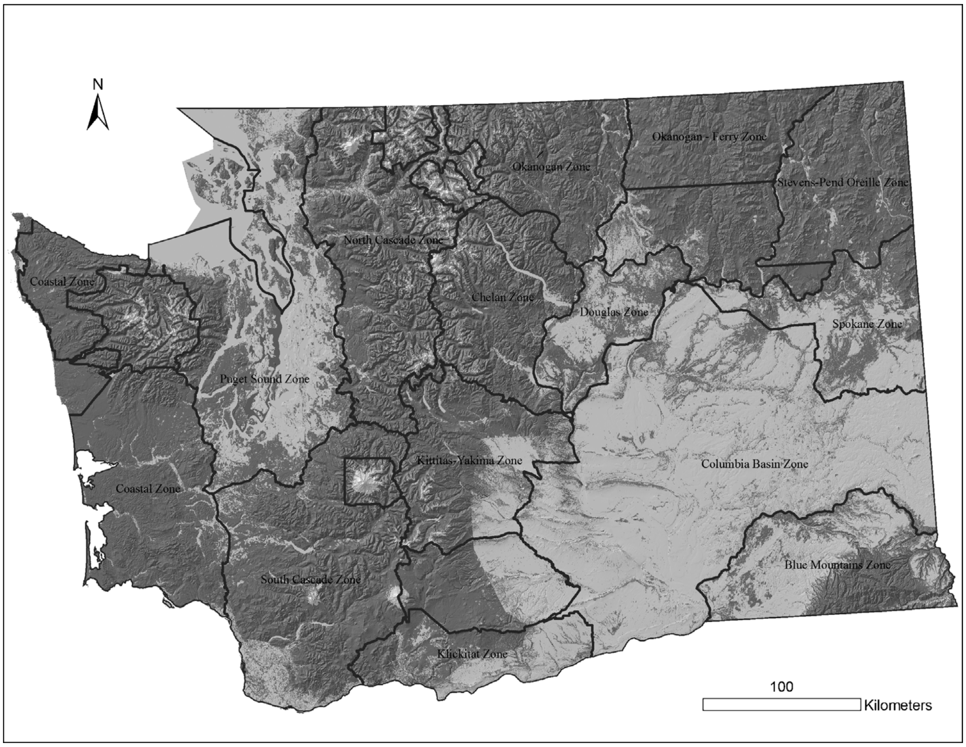

Figure 3. 2011 cougar management zones in Washington, USA, Washington Department of Fish and Wildlife, 2012.

for which juvenile status and sex are readily identifiable, most hunters are unable to distinguish female cougars from males and adults from subadults until after the animal is killed. Where the use of dogs is permitted, sex, and age determination may be more reliable but not certain due to restricted visibility of treed animals.

Many agencies employ a general open season and a permit-only season for cougar. Two concerns for hunters who participate in permit-only hunts (either limited-entry or quota hunts) are 1) when harvest threshold tallies begin during a general open season (which often overlaps with deer and elk season), and that, when filled, nullify the permit-only season; and 2) when the number of permits issued is greater than harvest threshold, thus creating a competitive atmosphere (the use it or lose it conundrum). In Washington, for example, 10–35 permits were issued for CMZs with harvest objectives for 6–20 cougars.

IMPLEMENTATION

The first step for applying our proposed management framework is to estimate the amount of cougar habitat. For Washington, we plotted 85,866 Global Positioning System and satellite telemetry locations from 117 radiocollared cougars in 5 study areas in to U.S. Fish and Wildlife Service–U.S. Geological Survey Landfire habitat coverage (LANDFIRE 2007) using ArcMap 9.3. We quantified the number of Global Positioning System locations in each habitat type, created a Geographic Information System data layer identifying habitats used by marked cougars, and extrapolated these habitats throughout the state. The result included 90,783 km^2 of the 104,000 km^2 of habitat for areas where WDFW has management authority (Fig. 1). For states and provinces lacking empirical estimation of suitable habitat for cougars, reliable and quantifiable estimates of forest cover, topographic variability, limited residential development (not to exceed exurban densities), and persistent ungulate prey may provide reasonable measure of suitable habitat for cougars (Burdett et al. 2010; Maletzke 2010; Kertson et al. 2011*b*). However, where existing Geographic Information System coverages may not reflect current landscape conditions, we advocate they be ground-truthed to avoid overestimating habitat. Including district or regional biologists and officers can also be advantageous.

We then overlaid current GMU boundaries onto this habitat coverage to calculate the available habitat within each GMU, and we applied adult densities of 1.7 cougars/100 km^2 to estimate the number of adult residents per GMU. Where GMUs were small (<750 km^2), or the habitat sparse, we combined adjacent GMUs; this resulted in 62 CMZs for Washington (Fig. 4). In jurisdictions where densities are not estimable, we suggest that the scientifically defensible average of 1.6 adults/100 km^2 be applied (Quigley and Hornocker 2010).

We applied a mean intrinsic rate of growth of 14% (Morrison 2010) to allocate harvest of adult cougar per unit of area (0.24 cougars/100 km^2 of habitat). For Washington, this resulted in a statewide annual harvest of 220 cougars, more than the average annual harvest from previous years. Although the proposed harvest would be greater, this harvest would be distributed more evenly across management units in the state, resulting in a more uniformly distributed hunter effort, less harvest clustering and population sinks, and

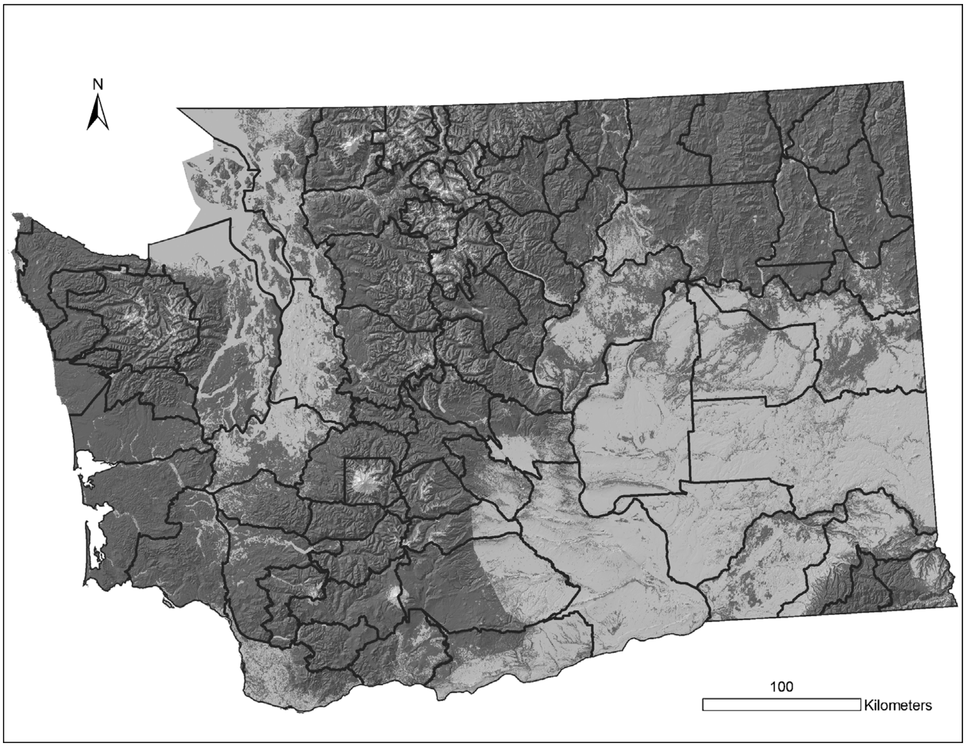

Figure 4. Proposed cougar management zones for Washington, USA, 2012.

greater stability in the cougar population. This strategy may prevent the need for harvest thresholds based on sex and could simplify harvest regulations and administration. We recommend using the harvest threshold of 14%. In addition, because subadult age classes are dynamic and difficult to estimate, and difficult to identify in the field, we recommend that harvest of this age class be counted against the allocated harvest so that recruitment is not affected in the future. Finally, we advocate administering the hunt using a 24-hour reporting and information hotline because it allows for prompt reporting of kills and CMZ closure and provides hunters the opportunity to plan hunt activity.

Administering harvest thresholds for GMUs or smaller CMZs has multiple benefits. It helps to 1) preserve the cougar's social organization by distributing harvest more evenly and avoiding creation of population sinks, 2) eliminate the need for harvest thresholds based on sex and for field identification of sex, 3) distribute hunter opportunity across the landscape, and 4) define a biological and meaningful spatial scale similar to that of their prey (ungulates), bringing management for predator and prey into alignment.

MANAGEMENT IMPLICATIONS

We acknowledge that these recommendations are based on research in Washington, but similar findings have been documented elsewhere in western North America (Quigley and Hornocker 2010). For the most part, current cougar management programs do not address the effects of harvest on social structure of cougar populations, a concept that was introduced >40 years ago (Hornocker 1969, 1970) and is supported by current research. We believe this science-based approach to cougar management is easy to implement, incurs no added costs, satisfies agency and stakeholder interests, and assures professional credibility. The current review of carnivore management has demonstrated a paradigm shift from lethal control to one of ecosystem management, and one that considers the values of multiple stakeholders and aspects of human dimensions (Treves 2009, Hornocker and Negri 2010, Van Ballenberghe 2011, Way and Bruskotter 2012, Peek et al. 2012). Our recommendations incorporating cougar behavior and social organization into a management framework addresses concerns of various constituencies, provides for quality hunter experience, and recognizes values of the non-consumptive public while maintaining viable cougar populations and the behavioral integrity of their populations.

A simple, consistent, science-based approach to cougar management can be of benefit to agencies during intervals of administrative and political uncertainty. In addition to fulfilling agency mandates for hunter opportunity, our proposal adheres to our state agency's mission to "promote development and responsible use of sound, objective science to inform decision making" (WDFW 2008). In our opinion, of equal importance is recognizing the ecological and evolutionary role of cougar in the trophic hierarchy (Estes et al. 2011); and incorporating this concept into management and education elevates the cougar's status beyond a mere predator.

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

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

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

INTRODUCTION

Density-dependent population regulation has been experimentally demonstrated for a variety of animals and forms the theoretical basis for sustainable hunting of polygynous mammals (Caughley 1977, Caughley and Sinclair 1994, Ginsberg and Milner-Gulland 1994, Strickland et al. 1994). The compensatory mortality hypothesis predicts that harvest mortality, especially of adult males, triggers density-dependent responses in reproduction, offspring survival, and female population growth by reducing competition for resources (Connell 1978). In unhunted or lightly harvested populations, higher densities generate increased competition for resources, resulting in decreased reproduction, offspring survival, and female population growth. Therefore, removal of adult males in polygynous mating systems is generally considered to have benign or beneficial effects on population growth (Errington 1945, Frank and Woodroffe 2001, Johnson et al. 2001).

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

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

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

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

STUDY AREAS

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

Heavily hunted area (HH)

The 735-km^2 study area lies north of the town of Kettle Falls, and includes a patchwork of federal, state, and privately owned lands. The study area is bounded on the southeast and southwest by the Columbia and Kettle Rivers. The Canadian–United States border forms the northern boundary. The area is part of a glacially subdued mountainous region (400–2130 m elevation) known as the Okanogan Highlands, and occupies the transition between the East-slope Cascades and Northern Rocky Mountain physiographic province (Bailey et al. 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the 46-cm annual precipitation falls as snow, with an average of 136 cm falling from mid-November to mid-April annually. Mean annual temperatures range from −6°C in January to 21°C in July. White-tailed deer (*Odocoileus virginianus*) are the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) are also present. Common predator species besides cougar include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*).

Lightly hunted area (LH)

The study area is located along the East-slope foothills of the North Cascades Mountains near the town of Cle Elum. The area covers 594 km^2 and includes a portion of the upper Yakima River watershed. The study area is bounded by the Cascade Mountains on the west, the Enchantment Wilderness on the north, and unforested agricultural lands of the Kittitas Valley on the south and east. Sagebrush steppe foothills (below 550 m elevation) transition upward to slopes covered with ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Psuedotsuga menziesii*). Subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) dominate ridges at elevations >1550 m. Precipitation averages 56.4 cm/yr, with 160 cm of snowfall during winter. Mean annual temperature ranges from −7°C in January to 27°C in July. Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species besides cougar include coyotes, black bears, and bobcats.

METHODS

Captures and monitoring

We attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of each study area during winter when tracks can be detected in snow. We used hounds to track and tree cougars (Hornocker 1970). We immobilized treed cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 mL/10 kg of body mass, or with Telazol at a dosage of 6 mg/kg, using a projectile dart in the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). We determined sex and classified animals as kittens (0–12 months), juveniles (13–24 months), or adults (25+ months) based on physical measurements and gum regression measurements of the canine teeth (Laundre et al. 2000).

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

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

Survival

We used radiotelemetry to monitor survival of all radio-collared cougars and assigned cause of mortality as hunting, vehicle, or natural. Natural mortalities were confirmed with necropsies. We inferred cause of kitten mortalities by examining the carcass and proximity to other collared cougars.

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

To determine intervals when survival probabilities were constant, we analyzed the statistical distribution of deaths over a 365-day period (Lambert et al. 2006). This yielded two mortality seasons: a high-mortality season (LH: 1 August to 31 December, HH: 1 October to 31 January) and a low-mortality season (LH: 1 January to 31 July, HH: 2 February to September 31). Annual survival was the product of seasonal survival rates (Heisey and Fuller 1985). We chose intervals for each period based on the median date of the deaths for each period. We used the Taylor series approximation method to compute variances of class-specific survival rates, and a one-tailed z test to determine whether survival rates in LH were higher than in HH (Micromort version 1.3; Heisey and Fuller 1985).

Maternity and fecundity

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

Deterministic and stochastic growth rates

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

We calculated the deterministic growth rate (λ_{D}) as the dominant eigenvalue of the matrix under a stable age distribution. We calculated the stochastic growth rate (λ_{S}) by incorporating annual environmental variability (standard deviation of annual survival and fecundity rates) and demographic stochasticity. To estimate demographic stochasticity, we sampled the number of survivors in each sex and age class from a binomial distribution, and the number of kittens born each year from a Poisson distribution using the random number generator in RAMAS GIS (Akçakaya 2002). We sampled vital rates from a lognormal distribution to avoid truncations, which can occur if standard deviations are large due to sampling and measurement error. We projected each population for six years (five transitions), and calculated λ_{S} as the average geometric mean growth rate from 200 simulations, the point at which rates converged (Robinson et al. 2008).

Observed growth, immigration, and emigration

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

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

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

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

and kittens) in each study area and calculated λ_O as $\lambda_x = (n_t/n_0)^{1/t}$, where λ_x is the annual finite growth rate, n_0 is the starting population, n_t is the final population, and t is the number of transitions between the start and end of the population projection (Case 2000). We used a one-tailed, one-sample t test to determine whether deterministic (λ_D) and stochastic (λ_S) growth rates were higher than the average six-year observed (λ_O) growth rate for LH, and whether λ_D and λ_S were lower than λ_O for HH (Zar 1999). We estimated net immigration/emigration rate (i/e) using the equations $i/e = \lambda_D - \lambda_O$ and $e = \lambda_S - \lambda_O$ (Peery et al. 2006). We also used observations of radio-collared cougars to document net emigration and immigration in each area from 2005 through 2007, the period during which we radio-monitored kittens (radio collars enabled us to document emigrants).

Population density

We estimated mean annual densities of cougars (number of cougars/100 km^2) for each study area as the number of animals multiplied by the mean proportion of male and female locations that fell inside a mean annual 95% composite kernel home range of collared females (McLellan 1989). For unmarked cougars, we used the mean proportion of marked animals. We back-calculated the life span of each marked and unmarked cougar to the beginning of the study, its birth date (females), or immigration date (males) as described by Logan and Sweanor (2001:66), Stoner et al. (2006), and Robinson et al. (2008). We used a general linear model (GLM) to test for independent effects of study area and time on cougar density. We included study area, time, time^2, time × study area, and time^2 × study area as independent variables and then selected variables stepwise in a backward fashion, removing those that failed to be significant at the 0.10 probability level (Zar 1999).

Age structure

We calculated sex ratios (F:M) from collared cougars only to prevent bias that may result from hunters selecting for male cougars (trophies). We determined whether ratios were different from equality with a chi-square goodness-of-fit test (Zar 1999). We compared mean age of cougars in each area with a two-sample t test and examined the trend over time in age structure with simple linear regression (Zar 1999).

Confounding factors

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

Results

Captures and monitoring

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

Survival and mortality

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

TABLE 1. Extended.

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

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

Average annual survival rates, including all sources of mortality, for all radio-collared cougars in HH were 0.56 ± 0.05 (mean ± SD) and 0.71 ± 0.06 in LH, but survival varied with age and sex classes (Table 2). Overall survival and survival of adults was higher in LH than in HH (overall: $Z = 1.98$, $P = 0.02$; adults: $Z = 1.75$, $P = 0.04$). Survival of adult females and survival of kittens was also higher in LH (adult females: $Z = 1.88$, $P = 0.03$; kittens: $Z = 1.49$, $P = 0.07$). We did not detect differences among other sex or age comparisons. Overall mortality rate from hunting was higher ($Z = 2.02$, $P = 0.04$) in HH (0.24 ± 0.05) than in LH (0.11 ± 0.04). We found no differences in natural mortality rates (HH = 0.18 ± 0.04, LH = 0.13 ± 0.04; $Z = 0.77$, $P = 0.44$). The standard deviation of annual survival rates, including all sources of mortality for all cougars, was 0.09 in HH and 0.06 in LH. These values were used in the standard deviation matrix of RAMAS. We removed the six kittens from the analysis that were killed by male cougars in HH, recalculated survival rates, and found that kitten survival was not different ($Z = 0.96$, $P = 0.96$) in HH (0.59 ± 0.02) and LH (0.58 ± 0.02).

Maternity and fecundity

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

Population growth

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

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

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

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

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

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

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

Population density

The mean 95% composite range of females was 772 km^2 (95% CI = 316–1228) for HH and 655 km^2 (95% CI = 425–885) for LH. The annual proportion (mean ± SD) of male GPS points within the composite range of females was 0.32 ± 0.08 in HH and 0.43 ± 0.16 in LH.

Time and time × area explained significant variation in cougar density ($P < 0.10$). The final model included: area, time, and time × area. Mean annual densities of all cougars were 3.46 ± 0.69/100 km^2 in HH and 3.62 ± 0.58/100 km^2 in LH, and were not different ($P = 0.26$) (Tables 3 and 4). Compared to LH, mean densities of males were lower in HH (0.63 ± 0.12 vs. 1.30 ± 0.15/100 km^2; $P < 0.01$) and mean densities of females were higher (2.83 ± 0.76 vs. 2.32 ± 0.44; $P = 0.02$). Within HH, densities of all cougars and females declined over the study period, whereas we detected no change in male densities. In LH, we did not detect a change in density for any sex and age class (all $P > 0.05$; Table 4).

Sex and age structure

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

Confounding factors

We detected no differences in mean maternity rates ($t = 2.26$, df = 9, $P = 0.94$), predation rates ($t = 0.79$, df = 34, $P = 0.44$), or population density ($t = 1.47$, df = 1, $P = 0.26$) between areas. The female predation rate in HH was 6.68 days/kill (Cooley et al. 2008) and 7.04 days/kill in LH (K. White, *unpublished data*).

DISCUSSION

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

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

TABLE 4. Effects of study area (hunting level) and time (2002–2007) on density estimates of cougars (cougars/100 km^2) using a general linear model.

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

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

Resource availability could have influenced vital rates; however, both populations were at similar densities (3.46 cougars/100 km^2 in the heavily hunted area and 3.62 cougars/100 km^2 in the lightly hunted area) and female predation rates were not different, suggesting that resources were similar between areas. Densities were maintained via a net immigration into the heavily hunted area and a net emigration out of the lightly hunted area. The net emigration could indicate poorer resources; however, kitten survival and female population growth were higher there, suggesting that this is not the case. The net immigration rate in the heavily hunted area could suggest better resources, but kitten survival and female population growth were lower there, also contrary to the compensatory mortality hypothesis.

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

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

Long-distance dispersal is common in cougars (Sweanor et al. 2000, Logan and Sweanor 2001, Stoner et al. 2006) and can help to maintain overall numbers by replacing harvest mortalities with animals dispersing from neighboring areas (Hanski 2001). Rebound from heavy hunter harvest by immigration has been documented in cougar populations elsewhere (Ross and Jalkotzy 1992, Logan et al. 1986, Logan and Sweanor 2001, Anderson and Lindzey 2005, Stoner et al. 2006, Robinson et al. 2008). As a consequence, harvest models based on compensatory mortality hypothesis are unable to accurately predict the responses of cougar populations to hunting.

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

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

It is unlikely that age structure ever stabilizes in long-lived species such as cougars, which may bias our estimates of deterministic growth. Because this lack of variability assumes a stable age distribution, we have little confidence that differences between deterministic growth rates and observed growth rates act as predictors of actual population growth and believe that differences between stochastic growth rates and observed growth rates more accurately project growth rates. Additionally, despite intense trapping efforts conducted each winter, we may have missed some cougars that were present on the landscape during the study, resulting in biased estimates of observed growth and subsequent net immigration and emigration rates. The addition of the same number of cougars each year would increase density estimates, but would not change the observed growth and emigration rates. A temporal bias, such as missing cougars only early in the study (most likely error), would yield an even lower true observed growth rate, whereas missing cougars only later in the study (least likely error) would yield a higher true observed growth rate. For example, a count of 10 cougars in 2002 and 11 cougars in 2003 would yield an observed growth rate of 1.10. If we missed three cougars in 2002, the true growth rate would have been 11/13, or 0.85. We have neither reason nor evidence to suspect that we missed more cougars as the study progressed, therefore any bias in our observed population growth rates is conservative.

CONSERVATION IMPLICATIONS

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

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APPENDIX

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

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

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Abstract

Wildlife agencies typically attempt to manage carnivore numbers in localized game management units through hunting, and do not always consider the potential influences of immigration and emigration on the outcome of those hunting practices. However, such a closed population structure may not be an appropriate model for management of carnivore populations where immigration and emigration are important population parameters. The closed population hypothesis predicts that high hunting mortality will reduce numbers and densities of carnivores and that low hunting mortality will increase numbers and densities. By contrast, the open population hypothesis predicts that high hunting mortality may not reduce carnivore densities because of compensatory immigration, and low hunting mortality may not result in more carnivores because of compensatory emigration. Previous research supported the open population hypothesis with high immigration rates in a heavily hunted (hunting mortality rate = 0.24) cougar population in northern Washington. We test the open population hypothesis and high emigration rates in a lightly hunted (hunting mortality rate = 0.11) cougar population in central Washington by monitoring demography from 2002 to 2007. We used a dual sex survival/fecundity Leslie matrix to estimate closed population growth and annual census counts to estimate open population growth. The observed open population growth rate of 0.98 was lower than the closed survival/fecundity growth rates of 1.13 (deterministic) and 1.10 (stochastic), and suggests a 12–15% annual emigration rate. Our data support the open population hypothesis for lightly hunted populations of carnivores. Low hunting mortality did not result in increased numbers and densities of cougars, as commonly believed because of compensatory emigration.

Introduction

Sport hunting is commonly used to manage populations of large herbivores, such as white-tailed deer *Odocoileus virginianus*, mule deer *Odocoileus hemionous*, elk *Cervus elaphus* and moose *Alces alces* (Bolen & Robinson, 2003; Sinclair, Fryxell & Caughley, 2006) based on the closed population paradigm (e.g. increased deaths = decreased numbers). Large carnivores such as cougars *Puma concolor*, black bears *Ursus americanus*, grizzly bears *Ursus arctos* and leopards *Panthera pardus* are similarly hunted for sport and population control, based on the same closed population paradigm (Treves & Karanth, 2003). Managers commonly believe that sport hunting is effective for reducing the size of carnivore populations, the amount of predation on game species and the number of human/carnivore conflicts (Strickland *et al*., 1994; Treves & Karanth, 2003).

Heavy hunting mortality (hunting mortality rate = 0.38/year) over a very large area (32 800 km^2) did result in a cougar population decline in the Selkirk Mountains of southern British Columbia, northern Idaho and northeastern Washington (Lambert *et al*., 2006). However wildlife agencies typically manage carnivore numbers in much smaller, localized game management units. Cougar-occupied game management units average 904 km^2 [standard deviation (SD) = 763, n = 133] in Washington State, with explicit harvest and management prescriptions for each. The effects of hunting at these smaller scales do not consider the potential influences of immigration and emigration on the outcome of those hunting practices (Cougar Management Guidelines Working Group, 2005: 42–44). Nonetheless, this closed population paradigm predicts that hunting will reduce animal numbers and densities, and human/carnivore conflicts within a game management unit (Strickland *et al*., 1994). The corollary is that light hunting pressure will increase numbers and densities of carnivores and human/carnivore conflicts.

However, long-distance intrinsic dispersal is an important aspect of carnivore population ecology (Chepko-Sade & Halpin, 1987; Howe, Davis & Mosca, 1991; Sweanor, Logan & Hornocker, 2000; Frank & Woodroffe, 2001; Zimmerman, Breitenmoser-Wursten & Breitenmoser, 2005; Whitman *et al.*, 2007). High rates of emigration can depress population growth, and high rates of immigration can increase population growth regardless of birth and death rates. Failure to consider these dynamics may preclude achievement of management objectives for carnivores.

Cougars are hunted for sport and population control throughout the western USA based on the closed population hypothesis (Cougar Management Guidelines Working Group, 2005: 71–82; Strickland *et al.*, 1994). However, young male cougars exhibit intrinsic, long-distance dispersal (Ross & Jalkotzy, 1992; Sweanor *et al.*, 2000; Logan & Sweanor, 2001), suggesting that the open population hypothesis may be more appropriate. A previous study showed that high hunting mortality of cougars (hunting mortality rate = 0.24) within a typically sized (766 km^2) game management unit (GMU 105) did not result in the expected population decline because of compensatory immigration. Those results supported the open population hypothesis in a heavily hunted cougar population in north-east Washington (Robinson *et al.*, 2008).

In this study, we test the open and closed population hypotheses for a lightly hunted (hunting mortality rate = 0.11) cougar population in a typically sized 655 km^2 management area from 2001 to 2007 in central Washington. We compare a closed population growth model based on survival/fecundity rates to open, observed rates of population growth over a 6-year period. We test whether low hunting mortality results in high population growth and increased densities, as commonly believed (closed population hypothesis) or if low mortality is counterbalanced by compensatory emigration (open population hypothesis), as predicted by Robinson *et al.* (2008).

Study area

The 655 km^2 study area, located on the east slope of the North Cascades near the town of Cle Elum, WA, was composed of a patchwork of public (US Forest Service, Washington Department of Fish and Wildlife, Washington Department of Natural Resources) and private lands, with rural residential development and agriculture dominating the valley bottoms. The study area was surrounded on three sides by contiguous cougar habitat that did not present a barrier to animal movements (home ranges of several animals straddled the border) (Fig. 1). The study area included the upper Yakima River watershed with the Cascade Range bordering the study area on the west, the Enchantment Wilderness to the north and agricultural lands in the Kittitas Valley to the south-east. Part of the Cascade Mixed Forest ecoregion (Bailey *et al.*, 1994), the area rises from sagebrush steppe, ponderosa pine *Pinus ponderosa* and Douglas fir *Psuedotsuga menziesii* in the foothills (550 m), to sub-alpine fir *Abies lasiocarpa*, Englemann spruce *Picea engelmannii*, silver fir *Abies amabilis* and western hemlock *Tsuga heterophylla* at higher elevations (1550 m). Average winter temperature from December to February is 1.2 °C and average summer temperature from June to August is 17.6 °C. Precipitation averages 56.4 cm year^{-1}, with the majority falling in winter as snow (average winter snowfall is 160 cm).

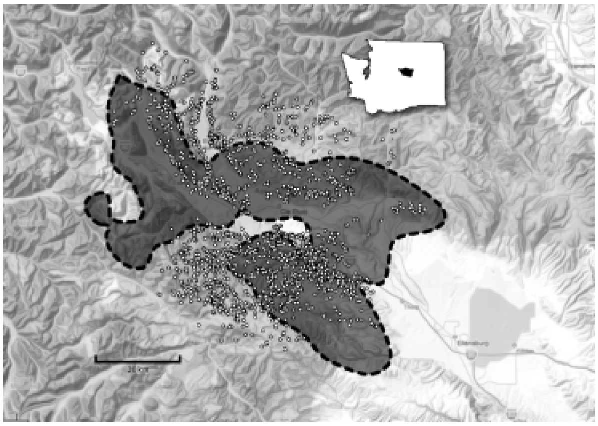

Figure 1 The central Washington study area showing the study area boundary defined by the 95% composite home range for female cougars *Puma concolor* (dashed line), and male global positioning system points (circles) used to calculate cougar densities. Contiguous cougar habitat and a lack of confining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

Elk and mule deer occur throughout the study area, and mountain goats *Oreamnos americanus* are present at higher elevations. Common predator species besides cougars include coyotes *Canis latrans*, black bears and bobcats *Lynx rufus*. Cougar harvest without the use of hounds was permitted in the study area each year of the study from 1 August to 15 March.

Methods

To allow comparisons with the heavily hunted population (Robinson *et al.*, 2008), we used the same methods for all aspects of this study.

Captures and monitoring

We attempted to capture and mark all cougars each year, from January 2002 through December 2007, by conducting thorough and systematic searches of the entire study area during winter when tracks are detected in snow. We used hounds to track and tree cougars in winter (Hornocker, 1970). We immobilized treed cougars with a mixture of ketamine hydrochloride (concentration level: 200 mg mL^{-1}) and xylazine hydrochloride (concentration level: 20 mg mL^{-1}), at a dosage of 0.4 mL/10 kg of body mass, using a projectile dart in the hindquarter (Ross & Jalkotzy, 1992; Spreadbury *et al.*, 1996). We determined sex by examining visible genitalia and age from measurements of gum regression (Laundre *et al.*, 2000) and assigned age classes as kitten (0–12 months), juvenile (13–24 months) and adult (25+ months).

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

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

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

Survival

We used radio telemetry to monitor survival of all radio-collared cougars and assigned cause of mortality as hunting, vehicle or natural. Natural mortalities were confirmed with necropsies. We inferred cause of kitten mortalities by examining the carcass and proximity to collared cougars.

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

We analyzed the statistical distribution of the deaths over a year (365 days) to determine the time intervals when survival probabilities were constant. This yielded two seasons: the high (1 August to 31 December) and the low mortality season (1 January to 31 July). Intervals for each period were chosen based on the median date of the deaths for each period. We used the Taylor series approximation method to compute variances of class-specific survival rates and tested for differences between classes with a two-tailed *z*-test (Micromort version 1.3, Heisey & Fuller, 1985).

Maternity and fecundity

We calculated maternity as the mean number of kittens divided by the number of adult females observed that year (Case, 2000). We calculated fecundity rate $F = S_F \times M_{x+1}$ from the female survival rate in year x multiplied by their mean maternity rate the following year (Ebert, 1999). To estimate annual environmental variation of fecundity rates, we calculated a weighted average of demographic variance and then subtracted it from the total observed variance (Akcakaya, 2002). This estimate minimizes sampling error and accounts for demographic stochasticity.

Deterministic and stochastic growth rates

We constructed a closed model of population growth from sex- and age-specific survival and fecundity rates and modeled population growth with a dual-sex Leslie matrix (Leslie, 1945) in RAMAS GIS (Akcakaya, 2002). Additional demographic parameters were: female age at first reproduction = 24 months; sex ratio at birth = 1:1; and maximum age and for age at senescence = 13 years (Logan & Sweanor, 2001).

We calculated the deterministic growth rate (λ_D) as the dominant eigen value of the matrix under a stable age distribution. We calculated the stochastic growth rate (λ_S) by incorporating annual environmental variability (SD of annual survival and fecundity rates) and demographic stochasticity. To estimate demographic stochasticity, we sampled the number of survivors in each sex and age class from a binomial distribution, and the number of kittens born each year from a Poisson distribution using the random number generator of RAMAS GIS (Akcakaya, 2002). We sampled vital rates from a log normal distribution to avoid truncations, which can occur if SD are large due to sampling and measurement error. We projected the population for 6 years (five transitions), and calculated λ_S as the average geometric mean growth rate from 200 simulations, the point at which rates converged (Robinson *et al.*, 2008).

Observed growth rate

We determined the observed growth rate (λ_O) from annual counts of collared and unmarked cougars. Each year we tallied the number of cougars (adults, juveniles and kittens) in the study area, and calculated the observed population growth rate, λ_O, as $\lambda_x = (n_t/n_0)^{1/t}$ where λ_x is the annual finite growth rate, n_0 is the starting population, n_t is the final population and t is the number of transitions between the start and end of the population projection (Case, 2000). We used a one-tailed, one-sample *t*-test (Zar, 1999) to determine whether deterministic (λ_D) and stochastic (λ_S) growth rates were higher than the average 6-year observed (λ_O) growth rate (Robinson *et al.*, 2008). Standard errors for mean λ_O were based on annual variation of λ_O from 2002 to 2007 ($n = 5$). We estimated emigration rate (e) using the equations $e = \lambda_D - \lambda_O$ and $e = \lambda_S - \lambda_O$ (Peery, Becker & Beissinger, 2006). We also used observations of radio-collared cougars to document emigration and immigration from 2005 through 2007, the period during which we had accurate kitten survival data.

Population density

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

Results

Captures and monitoring

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

Survival and mortality

Eighteen of 44 radio-collared cougars were killed during the study period. Seven were killed by hunters, three died in collisions with vehicles and six died of natural causes (Table 2). Six juvenile cougars (two females, four males) emigrated out of the study area and we censored these on their last known date in the area. We censored an additional seven animals after they shed their collars or lost VHF signals. We also censored one kitten that died 2 weeks after sustaining an injury during capture. Of 19 radio-collared kittens, nine survived to dispersal age of 18 months (five males, four females).

Average annual survival rate for all radio-collared cougars was 0.71 ± 0.06, but age and sex classes showed high variation (Table 3). Female survival (0.83 ± 0.07) was higher than male survival (0.60 ± 0.09, $Z = 2.16$, $P = 0.03$), and adult female survival (0.87 ± 0.07) was higher than adult male survival (0.65 ± 0.11, $Z = 1.71$, $P = 0.08$). We did not detect differences among other sex and age classes. We estimated environmental SD of survival for all collared cougars at 0.05. Mortality from hunting was 0.11 ± 0.04 and mortality from all combined causes was 0.19 ± 0.05.

Maternity and fecundity

We estimated mean litter size at 2.47 ± 0.83 from 15 litters. Proportion of females producing newborns was 0.45 and proportion of females with dependent kittens was 0.72. Mean maternity rate M_x was 1.12 kittens per female per year. The fecundity rate F_x was 0.49 ± 0.22 kittens of each sex per year. We estimated environmental SD of fecundity at 0.27 female kittens per year. Three female progeny were recruited into the population as adults, and we documented no recruitment from male progeny; all male progeny dispersed.

Population growth

The deterministic survival/fecundity growth rate (λ_D) was 1.13. The stochastic survival/fecundity growth rate λ_S was 1.10 ± 0.12 (mean ± SD). The observed growth rate (λ_O) based on the actual number of cougars in the study area was 0.98 ± 0.16. Both of our modeled growth rates were significantly higher than the observed rate (for λ_D, $t = 2.09$, $P = 0.05$; for λ_S, $t = 1.68$, $P = 0.09$). Observed growth rates of males ($\lambda_{OM} = 0.96 \pm 0.15$) and females ($\lambda_{OF} = 0.97 \pm 0.26$) were not significantly different ($t = 0.66$, $P = 0.54$). Emigration rates were 0.12 ($\lambda_O - \lambda$s) and 0.15 ($\lambda_O - \lambda_D$). Observations of radio-collared cougars supported the net emigration; we documented six emigrants (two female, four males) and three male immigrants from 2005 to 2007.

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

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

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

	Mortality source			
Sex and age class	*n*	Hunting	Vehicle	Natural
Female				
Kitten (0–12 months)	6			0.28 ± 0.24 (1)
Juvenile (13–24 months)	5	0.24 ± 0.21 (1)		
Adult (25 + months)	12	0.04 ± 0.04 (1)		0.09 ± 0.06 (2)
Female total	23	0.07 ± 0.05 (2)		0.10 ± 0.05 (3)
Male				
Kitten (0–12 months)	13			0.47 ± 0.17 (4)
Juvenile (13–24 months)	8	0.25 ± 0.22 (1)	0.25 ± 0.22 (1)	
Adult (25 + months)	12	0.20 ± 0.09 (4)	0.10 ± 0.07 (2)	0.05 ± 0.05 (1)
Male total	33	0.16 ± 0.06 (5)	0.09 ± 0.05 (3)	0.16 ± 0.06 (5)
Population total	56	0.11 ± 0.04 (7)	0.05 ± 0.03 (3)	0.13 ± 0.04 (8)

SD, standard deviation.

Table 3 Radio days, sample size (number of mortalities with total number of monitored animals in parentheses), and survival rates (mean ± SD) by sex and age class for radio-collared cougars *Puma concolor* near Cle Elum, WA, 2002–2007

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

SD, standard deviation.

Population density

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

Age structure

Mean age of the population was 41 months (3.4 years), mean age of adult males was 60 months (5 years), and mean age of adult females was 69 months (5.8 years). Mean age of all sex and age classes did not significantly change throughout the study period ($P > 0.10$).

Discussion

Cougar numbers and densities did not increase in response to low hunting mortality as predicted by the close population hypothesis. The closed population growth rates from survival and fecundity parameters ($\lambda_D = 1.13$, $\lambda_S = 1.10$) predicted an increasing cougar population, but we did not observe an increase in actual numbers ($\lambda_O = 0.98$). The difference between λ_D, λ_S and λ_O represents a 12–15% emigration rate; which was also supported by observations of net emigration of radio-collared cougars. Our findings reject the closed population hypothesis and support the open population hypothesis for typically sized game management units. Compensatory emigration appears to counter high survival/fecundity population growth in this study area. These results are consistent with Robinson *et al.*'s (2008) findings, whereby compensatory male immigration countered low survival/fecundity population growth in a heavily hunted cougar population.

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

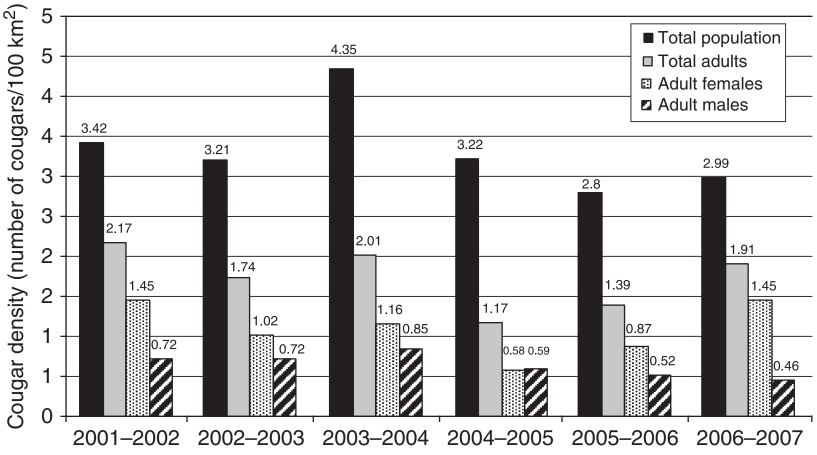

Figure 2 Total and adult cougar *Puma concolor* (>24 months old) densities (cougars/100 km^2) within the Cle Elum study area in central Washington, August 2001 to August 2007. Densities were calculated using the proportion of male and female locations that fell inside the mean annual 95% composite female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

growth and emigration rates – but simply increase density estimates. A temporal bias such as missing cougars only early in the study (most likely error because of relative trapping inexperience in the area) would yield an even lower true observed growth rate while missing cougars only later in the study (least likely error because of relative trapping experience in the area) would yield a higher true observed growth rate. For example, a count of 10 cougars in 2002 and 11 cougars in 2003 would yield an observed growth rate of 1.10. If we missed three cougars in 2002, the true growth rate would have been 11/13, or 0.85. We have neither reason nor evidence to suspect that we missed more cougars as the study progressed.

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

The comparable growth rates for males and females, and older ages of animals indicate that this population is stable. A younger age structure is characteristic of heavily hunted populations (Logan, Irwin & Skinner, 1986; Logan & Sweanor, 2001; Anderson & Lindzey, 2005) and may be indicative of a sink population where young males immigrate into available space (Robinson *et al.*, 2008). Stoner *et al.* (2006) documented significantly lower ages in a heavily hunted population than in an unhunted population [mean adult age of 40.8 months (3.4 years) in the hunted area and 55.2 months (4.6 years) in the unhunted area]. Robinson *et al.* (2008) also reported significantly ($P<0.05$) lower mean ages of adult females (46 months, 3.8 years) and adult males (41 months, 3.4 years) in a heavily hunted population, compared with a mean age of 69 months (5.8 years) for adult females and 60 months (5 years) for adult males in this study. The relatively low hunting mortality (0.11 ± 0.04) in this study compared with 0.24 ± 0.07 in northern Washington reported by Robinson *et al.* (2008) did not result in increased numbers and densities of cougars as might be expected.

The older age structure and associated territorial nature of resident animals in this population may limit immigration and enhance emigration of younger male animals. Logan & Sweanor (2001) found that adult males often exhibit territorial behavior, including repulsion of males through fighting, and exclusiveness of home ranges. The net emigration response of male progeny, along with recruitment of female progeny, and a positive stochastic growth rate, indicates that this population may be self-sustaining and may serve as a population source to the region (Thomas & Kunin, 1999; Sweanor *et al.*, 2000). Source emigration is a stabilizing force among metapopulations, can help sustain sink populations, and may contribute to an increase in the regional growth rate (Pulliam, 1988).

Implications for conservation and management

Our findings suggest that emigration counters high survival/fecundity population growth in this lightly hunted area. Low hunting mortality (0.11) did not result in increased numbers and densities of cougars (this study) and high hunting mortality (0.24) did not result in decreased numbers and densities of cougars (Robinson *et al.*, 2008) because of compensatory emigration and immigration responses. These metapopulation interactions appear to act as a stabilizing force to sub-populations (Pulliam, 1988; Sweanor *et al.*, 2000) in both the absence and presence of high hunting mortality, at least at the smaller game management unit scales (<1000 km^2) observed in these studies, and where prey density is adequate (Pierce, Bleich & Bowyer, 2000). Heavy hunting (mortality rate = 0.38) at a large scale (30 000 km^2) did cause a cougar population decline, probably because of lack of surviving emigrants in the entire region (Lambert *et al.*, 2006). Heavy hunting at all scales resulted in initial male population increase, a younger age structure and eventual female population decline (Lambert *et al.*, 2006; Robinson *et al.*, 2008).

Heavy hunting in typical management units ($<1000\,\mathrm{km}^2$) does not appear to correspond with decreased cougar numbers and densities (Robinson *et al.*, 2008), and low harvest rates in such units do not correspond with increased cougar numbers and densities as commonly believed. Immigration and emigration countered the population declines and increases predicted by the closed population hypothesis. These findings have two management implications: (1) cougar populations interact at landscape scales through immigration and emigration (metapopulations), so management at small scales may be inappropriate (Sweanor *et al.*, 2000; Stoner *et al.*, 2006; Robinson *et al.*, 2008) and (2) managers should incorporate rates of immigration and emigration in addition to survival and fecundity when developing harvest models for cougars and other large carnivores that exhibit open population structure at the game management unit scale.

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Effects of Remedial Sport Hunting on Cougar Complaints and Livestock Depredations

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Abstract

Remedial sport hunting of predators is often used to reduce predator populations and associated complaints and livestock depredations. We assessed the effects of remedial sport hunting on reducing cougar complaints and livestock depredations in Washington from 2005 to 2010 (6 years). The number of complaints, livestock depredations, cougars harvested, estimated cougar populations, human population and livestock populations were calculated for all 39 counties and 136 GMUs (game management units) in Washington. The data was then analyzed using a negative binomial generalized linear model to test for the expected negative relationship between the number of complaints and depredations in the current year with the number of cougars harvested the previous year. As expected, we found that complaints and depredations were positively associated with human population, livestock population, and cougar population. However, contrary to expectations we found that complaints and depredations were most strongly associated with cougars harvested the previous year. The odds of increased complaints and livestock depredations increased dramatically (36 to 240%) with increased cougar harvest. We suggest that increased young male immigration, social disruption of cougar populations, and associated changes in space use by cougars - caused by increased hunting resulted in the increased complaints and livestock depredations. Widespread indiscriminate hunting does not appear to be an effective preventative and remedial method for reducing predator complaints and livestock depredations.

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Introduction

Sport hunting is often used as a preventative or remedial measure to reduce carnivores and related human complaints and/or livestock depredations for many predators including, brown bears (*Ursus arctos arctos*) [1], cougars (*Puma concolor*) [2], grizzly bears (*Ursus arctos horribilus*) [3], jaguars (*Panthera onca*) [4], leopards (*Panthera pardus*) [5], lions (*Panthera leo*) [6], and others [7]. However, to our knowledge, the assumption that increased sport hunting reduces complaints and depredations has not been scientifically tested as yet [7].

For example, cougars (our model animal) have one of the broadest distributions of any mammal in the Western Hemisphere with a range that includes much of the North and South American continents [8]. This large, solitary carnivore is highly adaptable and occupies a wide variety of habitats [9]. Following European colonization of the Americas, their populations and range were diminished due to extensive harvest and population control through bounties - because cougars were often viewed as unacceptable threats to life and property [8].

After the bounty era ended cougars were still often viewed as potential threats to life and property. This view led to state management plans in the United States that were focused on reducing cougar populations to decrease cougar-human interactions primarily through increased sport hunting [10]. Many of these management plans based their cougar population estimates and harvest objectives solely (e.g. Washington Department of Fish and Wildlife until 2012) or in part on the number of complaints and depredations [10,11,12,13,14]. In Washington, as the number of complaints increased, the hunter effort and opportunity increased through lengthened seasons and higher bag limits - in response to what was thought to be a rapidly growing cougar population [10].

However, contrary to the public perception of increasing cougar populations, several areas with increasing numbers of complaints and depredations corresponded with declining female cougar populations and increasing male populations [2,15]. Heavy hunting (>25% per year) caused the female population growth rate to decline [2,15]. However, compensatory immigration [15] and emigration [16] by mostly males resulted in a stable observed growth rate with no net change in total cougar population size. Heavy remedial hunting of cougars simply changed the population age-sex structure towards younger immigrant male cougars in a source-sink dynamic [16]. The same phenomenon of increased male immigration and female decline with no net change in total numbers following increased hunting was also observed in grizzly bears populations [17,18,19]. These results suggest that remedial sport hunting might not reduce cougar (and other carnivore) populations and associated complaints and livestock depredations. In this paper we test the widely accepted hypothesis that increased

Table 1. Total reports collected for all 39 counties in Washington between Jan. 2005–May 2010.

Year	Verified Reports	Total Reports	Livestock Depredation	Total Depredation
2005	114	743	28	38
2006	88	581	32	42
2007	73	418	27	37
2008	63	408	30	34
2009	63	426	36	39
2010	31	110	13	19

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sport hunting will decrease cougar complaints and depredations in a large scale (statewide) long-term (6 years) observational experiment. The "remedial hunting" hypothesis predicts that complaints and livestock depredations will decrease following increased sport hunting. The "source-sink" hypothesis predicts that complaints and livestock depredations will remain stable, or even increase [2], following increased sport hunting.

Methods

Study Area

The state of Washington encompasses approximately 172,111 km^2 with natural regions ranging from a sea level coastal temperate rainforest to the Cascade mountain range to the Palouse prairie [20]. Cougars inhabited approximately 61% of the land mass of the state [21].

The Cascade Range reaches elevations of 4,395 m and divides the state into two distinct climate regions. The areas west of the Cascades have a temperate maritime climate characterized by mild wet winters and cool summers [22]. Average temperatures in the western regions of Washington range from 0°C in January to above 16°C in July. The areas east of the Cascade mountain range have a much drier climate with hot summers and much colder winters. Average temperatures in eastern Washington range from −18°C in January to 32°C in July. Forest vegetation covers approximately 51% of the total land area of Washington with the majority of forested regions located in the mountainous sections of Western and Northeastern Washington [22].

Data Collection

We collected data on numbers of people and numbers of cougars because these should be positively related to numbers of complaints. We also collected data on numbers of livestock and numbers of cougars because these should be positively related to numbers of depredations.

Finally, we collected data on numbers of cougars killed because these should be negatively related to the number of both complaints and depredations, according to the remedial hunting hypothesis.

Complaints and Depredations

We obtained the total number of cougar complaints from the Washington Department of Fish and Wildlife's Cougar Incident Database and categorized them based on the confidence level determined by agency staff (verified, possible, and unlikely). Verified cougar complaints and depredations were investigated and confirmed by Washington Department of Fish and Wildlife (WDFW) officers and only verified complaints were used in this analysis. Possible and unlikely complaints were not investigated or confirmed by WDFW officers and thus were not used in the analysis because those types of complaints (phone calls, verbal reports) could not be verified and appeared to be driven by socio-political, not biological factors [21,23]. Depredation events consisted of attacks or killings of domestic livestock and pets (*Canis lupus familiaris, Felis catus*) confirmed by WDFW officers. We refer to all depredations on domestic animals as "livestock depredations." We compiled the tallies for all 39 counties and 136 GMUs, in Washington for the six year time series (2005–2010), and removed all blank and duplicate cougar complaints.

Cougar Populations

We estimated the expected cougar population size for each county and GMU (game management unit) using an adult density of 1.7/100 km^2 and a total density of 3.5/100 km^2 for all cougar

Table 2. Basic descriptive statistics for county-level data from Washington, 2005–2010. Statistics shown are for the number of reports in each county for each year.

Factor	Minimum	Maximum	Range	Arithmetic Mean	Standard Error	95% Confidence Interval	Standard Deviation
Verified Reports	0	28	28	1.846	0.211	1.429–2.263	3.235
Livestock Depredations	0	11	11	0.709	0.105	0.503–0.916	1.602
Total Depredations	0	12	12	0.889	0.122	0.648–1.130	1.870
Population	2091	1931249	1929158	166894.551	21461.009	124612.122–209176.981	328290.305
Habitat (km^2)	190.447	11357.910	11167.463	2679.532	150	2384.002–2975.062	2294.562
Deer Sized Livestock	1549	139244	137695	18925.333	1555.954	15859.796–21990.871	23801.526
Small Sized Livestock	20	1510438	1510418	61626.205	16455.393	29205.828–94046.582	251719.109

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Table 3. Summary of best county-level model outputs.

Dependent variable	Independent Variable	Estimated Coefficient	Null Deviance	Residual Deviance	AIC	Standard Error
Verified Reports	Year	−0.248	337.30	228.09	761.68	0.178
	Cougar population	0.0084				
Livestock Depredations	Human population	1.789×10^{-2}	226.31	162.28	476.86	0.139
	Cougar population	4.36×10^{-2}				
	Large livestock	2.336×10^{-4}				
Total Depredations	Human population	1.583×10^{-2}	258.05	176.97	533.53	0.159
	Cougar population	4.137×10^{-2}				
	Large livestock	2.176×10^{-4}				

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habitat in Washington [21]. These estimates are for animals >2 years of age and were based on long term (1998–2013) replicated (6 study areas) research studies throughout the state, which showed little or no variation in density regardless of location, time or level of harvest [16,21].

Human Population

The number of people in each county and GMU during each year was obtained from the United States Census Bureau Quick Facts (2010). We converted the census data from census block polygons into centroids with the number of people per census block [23]. We then used a spatial join in ArcMap 9.3 to determine the number of people per GMU and calculated density by dividing by the area of each GMU (GMU mean area = 1232.62 km^2, standard deviation = 1103.55 km^2).

Livestock Numbers

The numbers of livestock were obtained from the United States Department of Agriculture National Agricultural Statistics Service for each county in Washington during 2005–2010 [24]. We tallied the livestock numbers and placed them into two categories for each county: large or deer-sized livestock and small livestock. The category for large or deer sized livestock consisted of alpacas (*Vigugna pacos*), llamas (*Lama glama*), cattle (*Bos primigenius*), equine (*Equus caballus*), goats (*Capra aegagrus*), hogs (*Sus scrofa*) and sheep (*Ovis aries*). Small livestock consisted of chickens (*Gallus gallus domesticus*), ducks (family Anatidae), geese (genus *Anser*), pheasants (*Phasianus colchicus*), and turkeys (*Meleagris gallopavo*). The numbers of livestock across the state were only available in summary form for each county and the boundaries were not consistent with GMUs-so we could only use livestock in the county-level analysis.

Cougars Harvested

We obtained the number of cougars harvested through sport harvest in each GMU each year from the Washington Department of Fish and Wildlife's Game Harvest Report Database (http://wdfw.wa.gov/hunting/harvest/). The numbers of cougars harvested across the state were only available by GMU and the boundaries were not consistent with the county boundaries so we could not use harvest in the county level analysis.

Because cougar harvest management is based on adult (>2 year old) density (1.7/100 km^2) in Washington (WA) [21], we calculated the proportion of cougars harvested in each GMU by taking the number of cougars harvested by sport hunters divided by the number of adult cougars estimated to be on the landscape for that GMU. We did not analyze the effects of depredation removals by WDFW personnel separately, because such livestock depredations were handled by issuing additional hunting permits to the landowner (allowing the use of tracking hounds) in response to the depredation [10].

Data Analysis

Statistical analysis. We used a negative binomial general linearized model to assess the relationship between verified reports and county- and GMU-level factors. The negative binomial error distribution was used rather than a Poisson error distribution to analyze our frequency data (complaints, depredations) because our dependent variables consisted of 0 to positive integer count data with a variance exceeding the mean [25]. A negative binomial general linearized model is appropriate for this type of over-dispersed count data with numerous zeros. We also tested a zero-inflated negative binomial model, which estimates regression coefficients for two components: one modeling the response

Table 4. Total reports collected for all 136 GMUs in Washington from January 2005 to May 2010.

Year	Verified Reports	Total Reports	Livestock Depredation	Total Depredation	Cougars Harvested
2005	111	674	28	37	182
2006	86	569	32	41	199
2007	72	416	28	38	198
2008	61	398	28	31	188
2009	63	416	37	40	140
2010	30	106	13	19	161

*107 total reports and 9 verified reports removed because no GMU was listed in the complaint.

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Table 5. Basic descriptive statistics for GMU-level tests. Statistics shown are for each GMU for each year.

Factor	Minimum	Maximum	Range	Arithmetic Mean	Standard Error	95% Confidence Interval	Standard Deviation
Verified Reports	0	11	11	0.526	0.042	0.443–0.608	1.197
Livestock Depredations	0	9	9	0.203	0.025	0.155–0.252	0.708
Total Depredations	0	10	10	0.255	0.027	0.201–0.309	0.782
Cougars Harvested	0	15	15	1.331	0.077	1.180–1.482	2.194
Habitat (km^2)	2.759	2713.761	2711.003	667.545	19.033	630.185–704.904	543.689
Proportion of Adult Cougars Harvested	0.000	1.9101	1.9100	0.117	0.007	0.103–0.132	0.210

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variable with a negative binomial distribution, and one component accounting for a disproportionate occurrence of zero values in the model [26]. However, goodness-of-fit tests indicated that the additional fitting precision associated with this method was unnecessary. The most appropriate statistical model was then selected using the AIC (Akaike Information Criterion) and log-likelihood values [27]. The rate ratio, analogous to odds-ratio, was computed from the coefficients to aid in interpreting the results [28]. For example, a rate ratio of 1.0 for any independent variable means the effect on the dependent variable is unchanged. A rate ratio of 1.5 means the odds are increased by 50%, a ratio of 2.0 means the odds are increased by 100% etc. Descriptive statistics for all variables and negative binomial regression models were generated for verified complaints, verified livestock depredations, and verified total depredations using the R environment for statistical programming [29].

County-based tests. The independent variables obtained from county data were human population, livestock numbers, and number of cougars. Complaints and depredations were the dependent variables. To determine which variables have a statistically significant relationship with cougar complaints and depredations we used a negative binomial generalized linear model (coefficients tested at $\alpha = 0.05$).

GMU-based tests. The independent variables obtained from GMU were number of cougars, number of cougars harvested, proportion of cougars harvested and human population. The number of livestock was not available by GMU, but comparing the odds ratio between the county and the GMU level tests allows for direct comparison of the relative effects of livestock compared to the other independent variables. For example, if the odds of a livestock depredation are increased from 1 to 1.5 with each additional livestock, and the odds of a depredation are increased from 1 to 2.5 with each additional cougar, we can conclude that the number of cougars has a larger effect than additional livestock on the probability of livestock depredations. To determine which factors have a statistically significant relationship with cougar reports and depredations we used a negative binomial generalized linear model (coefficients tested at $\alpha = 0.05$). In order to establish directionality of putative causation, we used the previous year's harvest and the following year's cougar complaints or depredations to determine statistically significant relationships. Cougar complaints and depredations were the dependent variables. We also tested for the effects of the previous 2–4 year time-lagged harvest, but those results are not reported here because they were almost identical to the 1 year time-lagged data presented here.

Results

County-based Tests

The total number of non-duplicated complaint reports between January 2005 and May 2010 was 2648; 432 reports were verified

Table 6. Summary of best GMU-level model outputs.

Dependent Variable	Independent Variable	Estimated Coefficients	Null Deviance	Residual Deviance	AIC	Standard Error
Verified Reports	Cougars harvested	0.308	496.17	422.43	1123.1	0.0697
	Cougar population	0.031				
Verified Reports	% cougars harvested	9.57×10^{-1}	444.32	416.63	1157.1	0.0510
	Human population	1.066×10^{-6}				
Livestock Depredations	Cougars harvested	0.428	310.00	253.63	644.87	0.0561
	Cougar population	0.038				
Livestock Depredations	% cougars harvested	1.216	268.75	247.24	668.72	0.0377
	Human population	1.278×10^{-6}				
Total Depredations	Cougars harvested	0.386	360.63	295.05	743.66	0.0647
	Cougar population	0.038				
Total Depredations	% cougars harvested	9.633×10^{-1}	310.50	288.64	775.32	0.0421
	Human population	1.164×10^{-6}				

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Table 7. Reports filed in Kittitas County, Washington from January 2005–May 2010.

	Verified Reports	Total Reports	Livestock Depredations	Total Depredations
2005	5	11	1	1
2006	3	9	1	1
2007	0	1	0	0
2008	0	3	0	0
2009	4	10	2	2
2010	1	4	0	1

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and 166 of those verified complaints were livestock depredations. Over the course of the 6-year time series, the number of total and verified cougar complaints generally declined while depredations remained relatively constant (Table 1,2). For a distribution map of reports by county across the state see supporting Figure S1.

The county-based model revealed that the primary factors influencing verified complaints were the year and total expected cougar population (Table 3, Results S1). However, each additional cougar on the landscape only increased the odds of a verified complaint by 1.00847 times or approximately 1%.

Several variables also influenced the number of livestock depredations at the county level including human population, the number of large livestock, and the total cougar population on the landscape. As the human population increased in an area the number of livestock depredations also increased in that area. With each increase in 10,000 people in an area the probability of a livestock depredation occurring in that area increased by 1.018 times or approximately 2%. For each additional 2000 large livestock in the area the chance of a livestock depredation occurring increased by 1.0002 times or less than 1%. For each additional cougar on the landscape the chance of a livestock depredation occurring increased by 1.0446 times or approximately 5%. For each additional 2000 large livestock in the area the chance of a livestock depredation occurring increased by 1.0002 times or less than 1%.

The final county-level model analyzed possible factors that influence the number of total verified depredations (livestock and pets). This model revealed that human population, the number of large livestock, and total cougar population present all are correlated with the number of depredations (Table 3). With each increase in 10,000 people in an area the probability of a depredation occurring in that region increased by 1.016 or approximately 2%. For each additional livestock animal the probability of a depredation being reported increased by 1.00022 times or less than 1%. For each additional cougar present the chance of a depredation occurring in that area increased by 1.042 or 4%.

Overall, the effects of numbers of people, livestock and cougars on the odds of total reports, verified reports, livestock depredation and total depredations were marginal, averaging from 1% to 5%.

GMU-based Tests

The total number of non-duplicated complaints between January 2005 and May 2010 was 2647; 429 complaints were verified and 166 of those verified complaints were livestock depredations. Over the course of 6 years the number of total and verified complaints generally declined while depredations remained relatively constant (Table 4). Descriptive statistics for all variables tested were also generated in statistical program R (Table 5). For the distribution of reports across the state by GMU see supporting Figure S2.

Two models were selected for determining which factors are related to the number of verified complaints in each GMU (Table 6, Results S1). The first model was $g(y) = -1.970170 + 0.308764$ (number of cougars harvested) $+0.031093$ (total cougar population) -0.003842 (cougars harvested*total cougar population).

The number of cougars harvested was positively related to the number of verified complaints per GMU (rate ratio = 1.36174, $z = 5.081$, $P < 0.001$). For each additional adult cougar harvested during the previous year the odds of a complaint increased by 1.36174 or 36%. The total expected population of cougars was also found to be positively associated with increased numbers of verified complaints (rate ratio = 1.03158, $z = 5.819$, $P < 0.001$). For each additional cougar on the landscape the odds of a verified complaint being filed increased by 1.03158 or 3%. The effect of cougars harvested the previous year on the odds of verified complaints is 10 times higher (1.36 vs 1.03) than the effect of number of cougars on the landscape.

Table 8. Reports filed in Stevens County, Washington from January 2005–May 2010.

	Verified Reports	Total Reports	Livestock Depredations	Total Depredations
2005	5	50	2	3
2006	8	47	4	5
2007	8	21	2	3
2008	3	25	1	1
2009	3	41	2	2
2010	9	15	5	8

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The second model selected for determining which factors may influence the number of verified complaints per GMU was g(y) = −1.081+0.9571 (proportion of adult cougars harvested) +1.066×10^{-6} (human population) +1.453×10^{-5} (proportion of adult cougars harvested*human population).

The proportion of adult cougars harvested was positively associated with the number of verified complaints (rate ratio = 2.60413, $z = 3.429$, $P<0.001$). For each 100% increase in harvest of adults the odds of a verified complaint the following year increased by a factor of 2.6 or 160%. Similarly for each 10% increase in harvest, the odds of a verified complaint increased by 16%. The number of people residing in each GMU was also positively related to an increased number of verified complaints (rate ratio = 1.000001066, $z = 2.285$, $P = 0.022$). For each additional 10,000 people in an area the chance of a verified complaint being filed increased by a factor of 1.000001066 or less than 1%.

Two models (Table 6) were also selected for determining which factors may be related to the number of livestock depredations in each GMU. The first model was g(y) = −3.155876+0.428854 (number of cougars harvested) +0.038094 (total cougar population) –0.005630 (cougars harvested*total cougar population).

Both of the main effects were found to be significant in this model. Once again, the number of adult cougars harvested was positively related to the number of livestock depredations in each GMU (rate ratio = 1.5355, $z = 5.097$, $P<0.001$). For each adult harvested the odds of a depredation went up by 53%. The total expected cougar population was also found to be positively associated with the number of verified livestock depredations (rate ratio = 1.03883, $z = 5.02$, $P<0.001$), but for each additional cougar on the landscape the odds of subsequent depredation went up only 4%.

The second model was selected to determine which factors may influence livestock depredations was g(y) = −2.019+1.216(proportion of adult cougars harvested) +1.278×10^{-6} (human population) +2.248×10^{-5} (proportion of adult cougars harvested*human population).

Both main effects were statistically significant in this model. The proportion of adult cougars harvested was positively related to the number of livestock depredations (rate ratio = 3.37367, $z = 3.186$, $P = 0.001$). The human population in each GMU was also significantly positively related to increased livestock depredations (rate ratio = 1.000001278, $z = 2.012$, $P = 0.044$). For each 100% increase in harvest rate of cougars (removal of all adult animals) the odds increased by a factor of 3.4 or 240%. Similarly a 10% increase in proportion of adult cougars harvested increased the odds of a livestock depredation occurring the following year by 24%.

The final models were selected to determine which factors influenced the number of total depredations (large and small livestock) reported in each GMU (Table 6). The model was g(y) = −2.910767+0.386019 (number of cougars harvested) +0.038721 (total cougar population) –0.005189 (cougars harvested*total cougar population). The main effects in this model were significant and positively associated with the number of total depredations. The number of adult cougars harvested had a rate ratio of 1.47111 ($z = 5.057$, $P<0.001$) while the total cougar population had a rate ratio of 1.03948 ($z = 5.716$, $P<0.001$). Once again for each adult cougar harvested the odds of a depredation occurring the following year were 1.5 or increased by 50%.

The other model selected for total depredations was g(y) = −1.753+0.9633 (proportion of adult cougars harvested) +1.164×10^{-6} (human population) +2.206×10^{-5} (proportion of adult cougars harvested*human population).

All of the main effects were significant in this model. The proportion of adult cougars harvested was positively related to the number of total depredations (rate ratio = 2.62, $z = 2.747$, $P = 0.006$). For each 100% increase in adult cougar harvested the odds of a depredation occurring the following year increased by 162%. Similarly for each 10% increase in resident adult cougar harvest the odds of a depredation being filed the following year increase 16%. The human population in each GMU was also marginally associated with total depredations (rate ratio = 1.000001164, $z = 1.999$, $P = 0.045$).

Discussion

Bases on our results, we reject the "remedial hunting" hypothesis and support the "source-sink" hypothesis on effects of sport hunting on complaints and livestock depredations. There were several different factors that influence the number of cougar complaints and depredations across the state of Washington. In increasing order of importance these include: the human population, the number of livestock, number of cougars, the number of cougars killed, and proportion of cougars killed. Consistent with expectations, each additional cougar on the landscape increased the odds of a complaint or livestock depredation by about 5%. However, contrary to expectations, each additional cougar killed on the landscape increased the odds by about 50%, or an order of magnitude higher. By far, hunting of cougars had the greatest effects, but not as expected. Very heavy hunting (100% removal of resident adults in 1 year) increased the odds of complaints and depredations in year 2 by 150% to 340%. It appears that remedial sport hunting to reduce complaints and depredations is actually associated with increased, not decreased, complaints and depredations the following year.

Increased hunting fails to account for compensatory immigration and the shift in the sex-age structure towards younger cougars, which may be responsible for the increased reports and depredations [2,15,16].

Within Washington, Robinson et al. [15] found that heavy hunting (25% mortality) resulted in increased compensatory immigration with a resulting abundance of younger males. By contrast, Cooley et al. [16] found that light hunting (10% mortality) and no hunting resulted in compensatory emigration by young males and a stable older male structure in the population. In the same areas, Maletzke [30] found that heavy hunting resulted in a doubling of male cougar home range size and home range overlap. All else being equal, this doubling of home range size should double the number of human-occupied areas in each male cougar's home range [30]. By the same token, each doubling of home range overlap should double the number of male cougars encountered by each human occupied area [30]. In addition, Kertson et al. [31,32,33] found that young cougars are more likely to be found in human-occupied areas then their older counterparts. Finally, Keehner [34] found that heavy hunting of cougars corresponded with females and kittens moving into sub-optimal habitats and killing sub-optimal prey species to avoid potentially infanticidal immigrant males. Elsewhere, Beier [35] found that juveniles and young adults may be responsible for the majority of the cougar-human conflicts in many areas and Torres et al. [36] found that male cougars are much more likely than females to engage in large livestock depredations. The above changes in sex/age structure and space-use by cougars following increased hunting could account for the observed increase in complaints and depredations in WA. We do not know which sex and age classes were responsible for the majority of complaints and depredations, but we do know that increased hunting was associated with increased, not decreased, complaints and depredations.

Our results are supported by a case study from two Washington cougar populations, where one was lightly hunted and one heavily hunted. The lightly hunted population (11±0.04 mortality rate) with a net male emigration rate of –12% [16], was located in Kittitas County (2478 mi^2) with an average 38,842 people, 21,441 large livestock, and 138 cougars. Kittitas County had an average of 6.33 total complaints/year, 2.12 verified complaints/year, 0.66 livestock depredations/year and 0.83 total depredations/year (Table 7). The heavily hunted (0.24±0.07 mortality rate) population with a net male immigration rate of +11%, was located in Stevens County (2,297 mi^2) and had 42,032 people, 22,293 large livestock and 207 cougars. Stevens County had an average number of 38.16 total complaints/year, 6.00 verified complaints/year, 2.66 livestock depredations/year, and 3.67 total depredations/year (Table 8). Stevens county had 1.5 times (50% more) as many cougars as Kittitas county, but had 3–6 times as many complaints and depredations. It appears the putative solution (heavy hunting) may have actually been exacerbating the problem in Stevens County.

Remedial hunting of cougars, in Washington, was associated with increased, not decreased, complaints and depredations. We encourage other researchers to test for the efficacy of remedial hunting on other carnivore species such as black bears, brown bears, grizzly bears, jaguars, leopards, lions and tigers to see if the source-sink hypothesis generalizes to those species as well.

Supporting Information

Figure S1 Average number of reports filed by county from Jan. 2005–May 2010 in Washington. Total reports, verified reports and verified livestock depredations averaged over the 5.5 year time frame (January 2005–May 2010) for each county in Washington.
(TIF)

Figure S2 Average number of reports filed by GMU from Jan 2005–May 2010 in Washington. Total reports, verified reports, and verified livestock depredations averaged over the 5.5 year time frame (January 2005–May 2010) for each GMU in Washington.
(TIF)

Results S1 Statistical program R outputs. Statistical program R outputs for all of the final models selected. Variables include: year (year2), cougar population (poptot), number of large livestock (livlarg), human population (humpop), the number of cougars harvested (hvst), and the proportion of adult cougars harvested (harvest_adlt).
(DOCX)

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Author Contributions

Conceived and designed the experiments: KP RW BM MS. Performed the experiments: KP RW BM. Analyzed the data: KP RW BM MS. Contributed reagents/materials/analysis tools: KP RW BM MS. Wrote the paper: KP RW BM MS.

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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 km^2) has reduced densities, hunting of smaller areas (i.e., game management units, $<$1000 km^2), could conceivably fail because of increased immigration from adjacent source areas. We monitored a heavily hunted population from 2001 to 2006 to test for the effects of hunting at a small scale ($<$1000 km^2) and to gauge whether population control was achieved ($\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 km^2) 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 Sweanor 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, Sweanor 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 ($>$2000 km^2) can reduce cougar densities (Lambert et al. 2006), hunting of small areas ($<$1000 km^2), 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 km^2) 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.

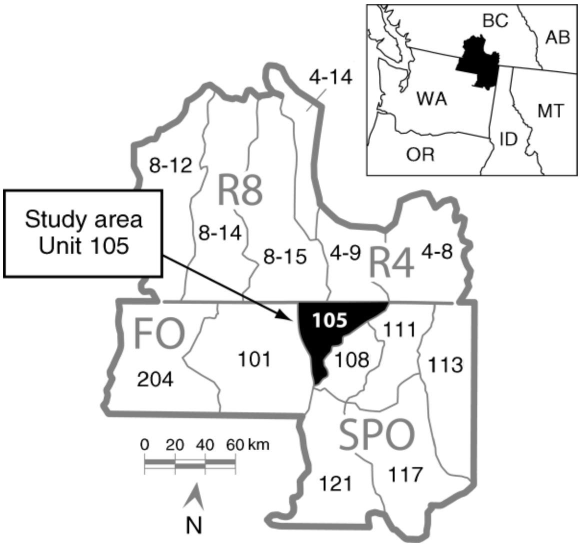

FIG. 1. Study area (Game Management Unit 105) surrounded by the Ferry-Okanogan (FO) and Stevens-Pend Orielle (SPO) cougar management zones of Washington State, USA, and by Region 4 (R4) and Region 8 (R8) of British Columbia (BC), Canada. Cougar management zones and Wildlife Regions are composed of smaller 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 km^2. 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 (Sweanor 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 ($\geq$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 Sweanor 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 Sweanor 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

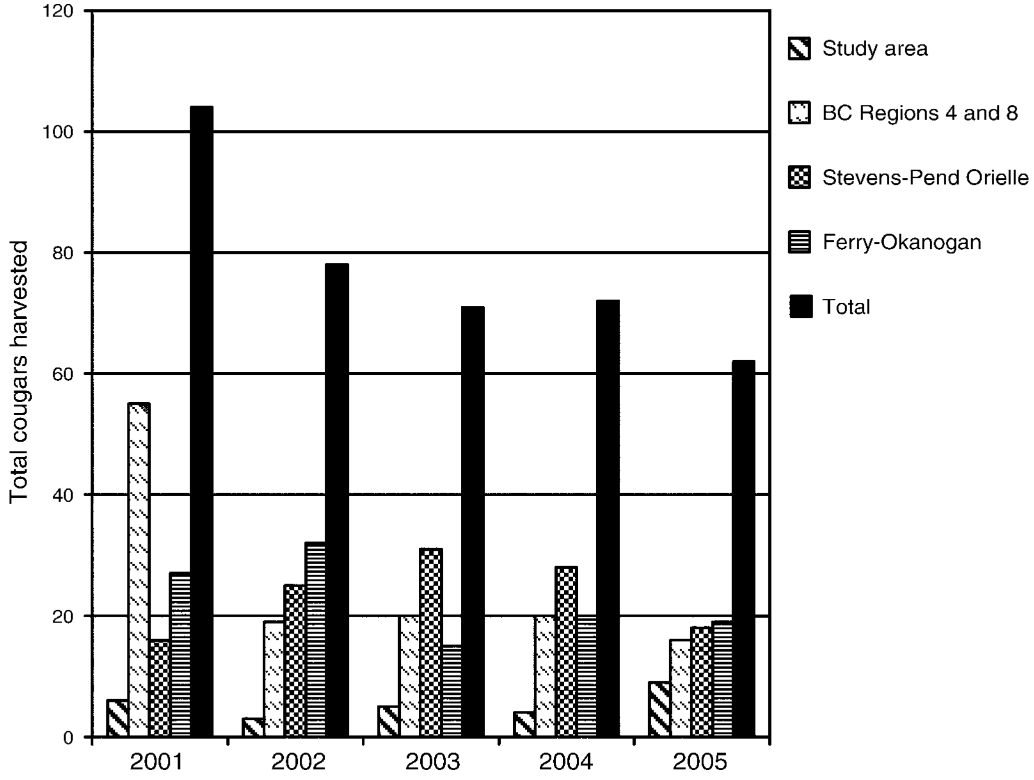

FIG. 2. Total cougar harvest (all ages and both sexes) for the years 2001–2005 in the study area and neighboring region, including Washington State's Ferry-Okanogan and Stevens-Pend Orielle Cougar Management Units and portions of British Columbia's Regions 4 and 8 (see also Fig. 1).

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 ± SD) by sex and age class for 34 radio-collared cougars (*Puma concolor*) in northeast Washington State, USA, 2002–2006.

	Females			Males		
Age class	No. radio-days	No. dead	Survival rate	No. radio-days	No. dead	Survival rate
Juvenile (13–24 months)	698	1	0.5926 ± 0.31	785	1	0.6280 ± 0.29
Subadult (25–36 months)	2039	1	0.8360 ± 0.15	1083	2	0.5093 ± 0.24
Male adult 4+ (37–108 months)				1018	3	0.3405 ± 0.21
Female adult 4–6 (37–60 months)	3530	3	0.7332 ± 0.13			
Female adult 6+ (61–108 months)	1883	2	0.6785 ± 0.19			
Total (all ages)	8150	7	0.7308 ± 0.09	2886	6	0.4678 ± 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 ± 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 ± 0.31 (1)
Subadult (25–36 months)		0.1639 ± 0.15 (1)	
Adult 4–6 (37–60 months)		0.1778 ± 0.11 (2)	0.0889 ± 0.08 (1)
Adult 6+ (61–120 months)		0.1607 ± 0.14 (1)	0.1607 ± 0.14 (1)
Female total		0.1538 ± 0.07 (4)	0.1153 ± 0.06 (3)
Male			
Juvenile (12–24 months)		0.3720 ± 0.29 (1)	
Subadult (25–36 months)		0.4906 ± 0.24 (2)	
Adult 4+ (37–120 months)	0.2198 ± 0.19 (1)	0.4396 ± 0.23 (2)	
Male total	0.0887 ± 0.08 (1)	0.4434 ± 0.14 (5)	
Population total	0.0268 ± 0.02 (1)	0.2420 ± 0.07 (9)	0.0806 ± 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 ± 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 ± 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 ± 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 km^2 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 km^2 to nine individuals in 2005 or 1.22/100 km^2 ($F = 1.66$, $P = 0.33$, $R^2 = 0.45$), while adult female density remained constant between 13 individuals or 1.77/100 km^2 and 10 individuals or 1.36/100 km^2 ($F = 0.71$, $P = 0.49$, $R^2 = 0.26$). The total adult density (males and females >24 months) also remained constant ranging from 17 individuals or 2.32/100 km^2 in 2001–2002 to 19 individuals or 2.58/100 km^2 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

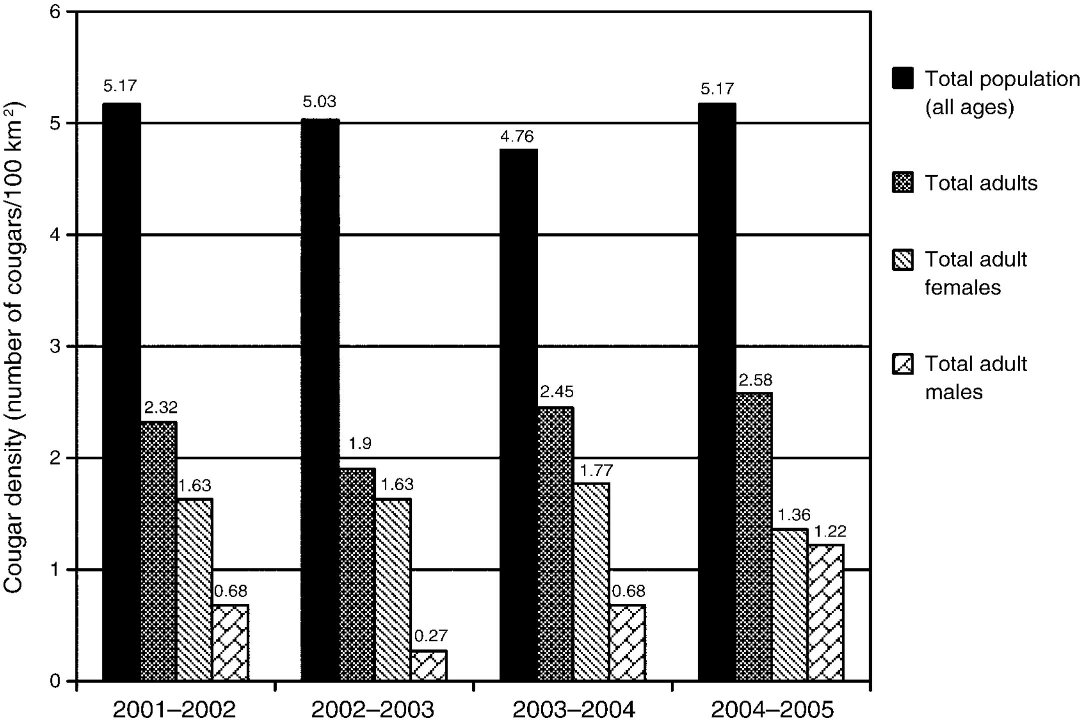

FIG. 3. Total and adult cougar (>24 months old) densities (density values given above bars) within the study area in northeastern Washington State, August to August 2001–2005.

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 km^2) 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)

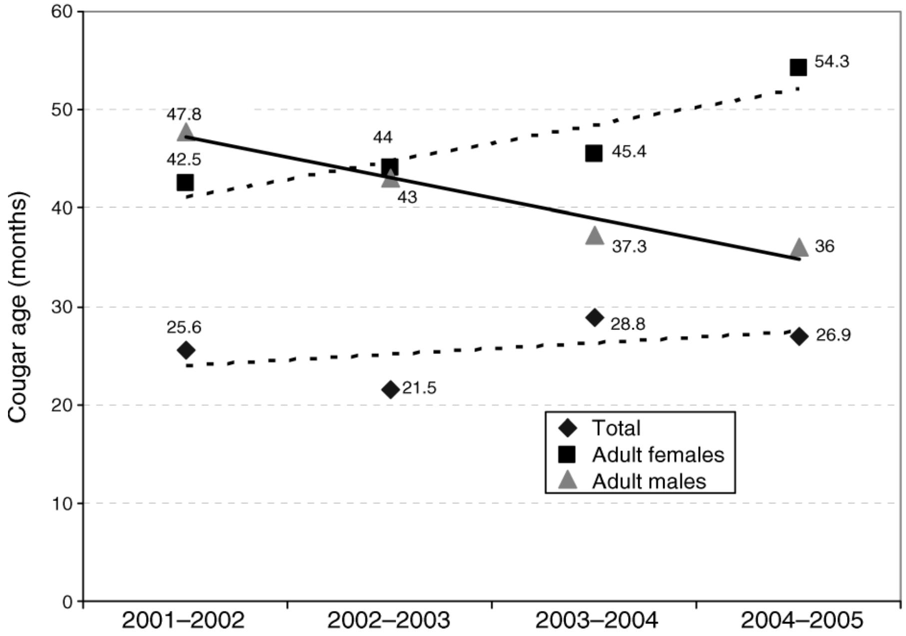

FIG. 4. Mean age (values given next to symbols) of the total population, independent adult females (>24 months old), and independent adult males (>24 months old) of a cougar population in northeastern Washington State, 2001–2005 (a solid line denotes a significant [$P < 0.05$] regression for adult males; 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 km^2) within part of the larger Stevens-Pend Orielle cougar management zone (total area 9131 km^2) (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 Sweanor (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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Cougar Exploitation Levels in Utah: Implications for Demographic Structure, Population Recovery, and Metapopulation Dynamics

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Abstract

*Currently, 11 western states and 2 Canadian provinces use sport hunting as the primary mechanism for managing cougar (*Puma concolor*) populations. Yet the impacts of sustained harvest on cougar population dynamics and demographic structure are not well understood. We evaluated the effects of hunting on cougar populations by comparing the dynamics and demographic composition of 2 populations exposed to different levels of harvest. We monitored the cougar populations on Monroe Mountain in south-central Utah, USA, and in the Oquirrh Mountains of north-central Utah from 1996 to 2004. Over this interval the Monroe population was subjected to annual removals ranging from 17.6–51.5% (mean ± SE = 35.4 ± 4.3%) of the population, resulting in a >60% decline in cougar population density. Concurrently, the Oquirrh study area was closed to hunting and the population remained stationary. Mean age in the hunted population was lower than in the protected population ($F = 9.0$; $df = 1, 60.3$; $P = 0.004$), and in a pooled sample of all study animals, females were older than males ($F = 13.8$; $df = 1, 60.3$; $P < 0.001$). Females from the hunted population were significantly younger than those from the protected population (3.7 vs. 5.9 yr), whereas male ages did not differ between sites (3.1 vs. 3.4 yr), suggesting that male spatial requirements may put a lower limit on the area necessary to protect a subpopulation. Survival tracked trends in density on both sites. Levels of human-caused mortality were significantly different between sites ($\chi^2 = 7.5$; $P = 0.006$). Fecundity rates were highly variable in the protected population but appeared to track density trends with a 1-year lag on the hunted site. Results indicate that harvest exceeding 40% of the population, sustained for ≥4 years, can have significant impacts on cougar population dynamics and demographic composition. Patterns of recruitment resembled a source–sink population structure due in part to spatially variable management strategies. Based on these observations, the temporal scale of population recovery will most likely be a function of local harvest levels, the productivity of potential source populations, and the degree of landscape connectivity among demes. Under these conditions the metapopulation perspective holds promise for broad-scale management of this species.* (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1588–1600; 2006)

Key words

connectivity, cougar, demographics, hunting, metapopulation, population dynamics, Puma concolor, *radiotelemetry, refuge, source–sink dynamics, Utah.*

Across western North America sport harvest is the primary mechanism for the population-scale management of *Puma concolor* (Pierce and Bleich 2003). Management regimes vary from public safety and depredation control only in California, to a year-round open season in Texas (Nowell and Jackson 1996). In order to balance hunting opportunities with protection of big game and livestock, most states manage cougar populations at some intermediate level. However, cougars are secretive, long-lived, and utilize large home ranges, making them difficult to manage with precision (Ross et al. 1996). At present, there are no widely accepted methods for the enumeration of cougars across diverse habitat types and climatic regimes (Anderson et al. 1992, Ross et al. 1996). Most techniques (e.g., track counts, scent stations, probability sampling) have limitations that render them marginally useful (Choate et al. 2006) or capable of detecting only large and rapid changes in population size (Van Sickle and Lindzey 1992, Beier and Cunningham 1996). Additionally, cougars occur at low population densities relative to their primary prey, making them sensitive both to bottom-up (e.g., prey declines; Logan and Sweanor 2001, Bowyer et al. 2005) and top-down (e.g., overexploitation; Murphy 1998) perturbations. Assessing cougar population trends is complicated by annual removals of varying intensity. Changes in population size and composition are generally indexed through harvest data and are therefore confounded by nonrandom sampling biases, further hindering reliable trend estimation (Wolfe et al. 2004).

Cougar management in Utah is spatially organized, with 4 broad ecoregions subdivided into 30 different hunting units. Each unit is managed independently in order to apply harvest pressure according to local priorities, which can include density reductions aimed at increasing survival in mule deer (*Odocoileus hemionus*) or bighorn sheep (*Ovis canadensis*) populations. Cougars are therefore managed at 2 different spatial scales. Locally, they are either managed conservatively as a trophy species or liberally as a limiting factor in the population dynamics of native ungulates. The statewide population, however, is managed for sustainable

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hunting opportunities and persistence across its currently occupied range (Mason et al. 1999).

Cougar hunting in Utah is conducted by means of pursuit with trained hounds. The hunting season extends from mid-December to early June, but approximately 75% of the kill occurs during December to March, when snow cover facilitates tracking and pursuit (Mason et al. 1999). Prior to 1998 the sport harvest of cougars occurred under a Limited Entry (i.e., lottery) system in which the number of permits for individual units is restricted. The long-term mean hunter success for this system is 64%. Beginning with the 1997–1998 season the Harvest Objective (i.e., quota) system was introduced for some units. This system employs an unlimited availability of permits to achieve a prescribed level of kill. Hunters are required to report their kill within 48 hours and the unit is closed once the quota is reached. Typically 74% of the quota is achieved, but instances of overharvest do occur. Between 1995 and 2003 legal harvest accounted for 90.0% of the total statewide cougar kill (Hill and Bunnell 2005). The remaining known mortality was distributed among animals killed in response to livestock depredation (6.2%) and other human-caused mortality, including roadkill and accidental trappings (3.8%). Additional unreported mortality such as incidental take during big game hunting seasons and illegal snaring occurs, but the magnitude of this impact is probably small relative to legal harvest. Individual cougars involved in livestock depredation are managed by the Wildlife Services Division of the United States Department of Agriculture, who may employ foot-hold snares as well as hounds to remove offending individuals. Nuisance cougars are defined as animals in urban settings that constitute a potential threat to human safety. These animals are generally controlled by Utah Division of Wildlife Resources (UDWR) personnel using lethal or nonlethal means, as circumstances warrant.

Little is known about both the immediate and long-term effects of sustained harvest on cougar populations (Anderson 1983, Ross et al. 1996). Numerous studies have been conducted on exploited populations (Murphy 1983, Barnhurst 1986, Logan et al. 1986, Ross and Jalkotzy 1992, Cunningham et al. 2000), including 2 removal experiments (Lindzey et al. 1992, Logan and Sweanor 2001), but few of these studies directly addressed the questions of: 1) how harvest affects the demographic structure of a population, and 2) what the long-term implications are for persistence and recovery of exploited populations within a metapopulation context. Moreover, habitat configuration and connectivity are important factors influencing cougar recruitment patterns, but with few exceptions (Beier 1993, 1995, Maehr et al. 2002) this relationship has been largely overlooked.

Recent years have seen the emergence of the idea of managing cougars as a metapopulation based on the effects of natural habitat patchiness (Sweanor et al. 2000, Laundré and Clark 2003) or anthropogenic fragmentation (Beier 1996, Ernest et al. 2003). Because metapopulations transcend administrative boundaries, understanding population response to sustained harvest is vital in order to manage for persistence across landscapes exhibiting varying degrees of natural and human-caused fragmentation.

We assessed the impacts of exploitation on cougar population dynamics by comparing demographic characteristics between an exploited and a semiprotected population. Specific objectives of this study were: 1) determine how harvest levels might influence the dynamics and demographic structure of individual populations, 2) identify the factors that may influence the rate of population recovery, and 3) assess how the distribution of harvest impacts might affect recruitment within a metapopulation context.

Study Area

Cougar habitat in Utah is geographically fragmented, being broadly associated with mesic regions between 1500 m and 3000 m. The Wasatch Mountains and associated high plateaus form the core habitat, longitudinally bisecting the state, whereas the Colorado Plateau and Great Basin ecoregions consist primarily of desert ecosystems, with suitable habitat sparsely distributed among insular mountain ranges (Fig. 1). We selected Monroe Mountain and the Oquirrh Mountains as study areas for this research (Fig. 1). Although differences existed between these sites in terms of size and plant community composition, they were located within 190 km of each other, making them climatically and ecologically similar in a broad sense, but far enough apart to be treated demographically as independent populations. The most pronounced difference between these populations was the level of exploitation to which each was subjected.

Exploited Area

Monroe Mountain comprises part of the Sevier Plateau in the Southern Mountains ecoregion of south-central Utah (38.5°N, 112°W). The site is a high volcanic plateau extending 75 km in a north–south orientation and lies within a west–east geologic transition from basin and range topography to the Colorado Plateau. Hydrologically, Monroe is part of the Great Basin, but climatically and biologically it is more closely associated with other high-elevation regions of the Colorado Plateau and southern Rocky Mountains. The study site covered approximately 1,300 km^2 and encompassed the central unit of the Fishlake National Forest, southeast of Richfield. Other landholders included the Bureau of Land Management (BLM), State of Utah, and various private interests.

The terrain is mountainous with elevations ranging from 1,600–3,400 m. Annual precipitation ranged from 15–20 cm at lower elevations to 60–120 cm on the plateaus above 2,700 m. Approximately 60% of the annual precipitation occurred as snow in January and February, with most of the remainder derived from summer thunderstorms (Ashcroft et al. 1992). Snowpack typically persisted until mid-June at elevations $>3,000$ m. Mean monthly temperatures ranged from $-4.6°$ C in January to 18.7° C in July (Ashcroft et al. 1992).

Plant communities were diverse and varied with elevation and aspect (Edwards et al. 1995). Piñon-juniper woodlands

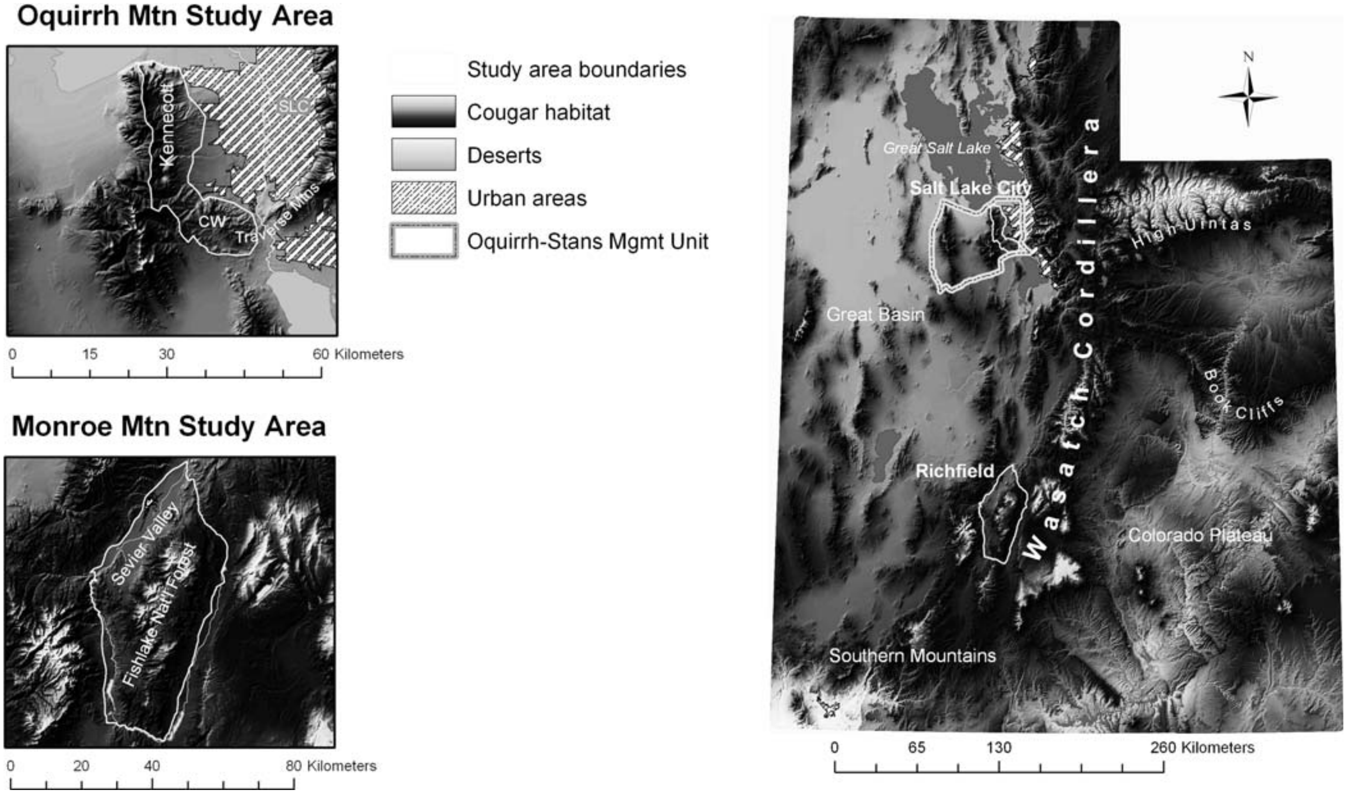

Figure 1. Study-area locations and cougar habitat across Utah, USA, 1996–2004.

(*Pinus edulis, Juniperus scopulorum, Juniperus osteosperma*) comprised the single largest vegetation type covering approximately 44% of the area. Mixed conifer and aspen (*Populus tremuloides*) stands occurred at higher elevations, with gambel oak (*Quercus gambelii*), mountain shrub (e.g., *Cercocarpus ledifolius, Rosa woodsii, Purshia tridentata*), and mixed sagebrush (*Artemisia tridentata*) –grassland meadows interspersed throughout.

Resource exploitation included livestock grazing, logging, and recreation. The UDWR classified Monroe Mountain as Cougar Management Unit 23. Mule deer and elk (*Cervus elaphus*), the primary cougar prey species on this site, were also managed for annual harvests. Human densities around the site varied from 73/100 km^2 to 382/100 km^2 (U.S. Census Bureau), with most of the population scattered among small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.

Protected Area

The Oquirrh-Traverse Mountains complex (hereafter the Oquirrhs) extends 55 km in a north–south orientation on the eastern edge of the Great Basin ecoregion in north-central Utah (40.5°N, 112.2°W). The Oquirrhs are typical of other mountain ranges within this ecoregion in that they form islands of high productivity relative to the surrounding desert basins (Brown 1971) and thus represented the majority of cougar habitat in this area.

The total area of the Oquirrhs measures approximately 950 km^2, but we conducted fieldwork primarily on the northeastern slope of the range on properties owned and managed by the Utah Army National Guard (Camp Williams, Traverse Mountains, 100 km^2) and the Kennecott Utah Copper Corporation (Oquirrh Mountains, 380 km^2). The site was situated at the southern end of the Great Salt Lake, abutting the southwestern side of the greater Salt Lake metro area. Ownership on the southern and western portions of the Oquirrhs was a conglomeration of BLM, grazing associations, and small mining interests, with approximately 45% of the range residing in private ownership.

Elevations on the site vary from lake level at 1,280 m up to 3,200 m. The Traverse Mountains run perpendicular to the Oquirrhs, and range in elevation from 1,650 m to 2,100 m. Annual precipitation ranged from 30–40 cm in the Salt Lake and Tooele valleys to 100–130 cm on the highest ridges and peaks. Most precipitation fell as snow between December and April, with approximately 25% occurring in the form of summer thunderstorms. Mean monthly temperatures ranged from −2.4° C in January to 22.2° C in July (Ashcroft et al. 1992).

Gambel oak and sagebrush were the predominant vegetation on the site. Also prevalent were Utah juniper in the foothills, and canyon maple (*Acer grandidentatum*) in the drainages at low elevations, and across broader areas above 1,800 m. Mountain mahogany (*Cercocarpus spp.*) was present, but relegated to well-drained soils along ridges. North-facing slopes above 2,200 m supported localized montane communities of aspen and Douglas fir (Edwards et al. 1995).

Mining activities have dominated the Kennecott property for >100 years (Roylance 1982), and the site included 2 large open pit mines and attendant infrastructure. Camp Williams was used for military training activities, and consequently exhibited brief fire return intervals. All prominent peaks on the study site supported commercial radio and television transmitters with associated access roads. A limited amount of livestock grazing occurred seasonally. Mule deer and elk were present on this study area as well; however deer were not hunted, whereas elk were subject to intensive management through annual harvests and active translocation projects. The study site was part of the Oquirrh-Stansbury Cougar Management Unit 18, but both of these properties were closed to the public and cougar hunting was prohibited. Human density adjoining the study area varied from 232/100 km^2 in rural Tooele County to 47,259/100 km^2 in urban Salt Lake County (United States Census Bureau).

Methods

We monitored cougar populations within the 2 study areas simultaneously from early 1997 to December 2004. We estimated demographic parameters for each population based on radiotelemetry data collected between 1996 and 2004 on Monroe and from 1997 and 2004 on the Oquirrhs. We calculated estimates of life-history parameters for cougars on the Oquirrh site during 1997 and 1998 from raw data presented in Leidolf and Wolfe (Utah State University, unpublished data). We performed statistical comparisons with the use of SAS (V.8) software. We report all descriptive statistics as mean ± SE unless otherwise noted.

Radiotelemetry and Harvest

We conducted intensive capture efforts during winter (Nov–Apr) each year of the study. We captured cougars by pursuing them into trees, culverts, cliffs, or mine shafts with trained hounds (Hemker et al. 1984). We immobilized each animal with a 5:1 combination of ketamine HCl and xylazine HCl (Kreeger 1996) at a dose of 10 mg ketamine plus 2 mg xylazine/kg of body weight. We administered immobilizing drugs with a Palmer CO_2 pistol (Powder Springs, Georgia), jab stick, or hand-held syringe. We collected tooth (vestigial premolar, P2) samples for age determination by counts of cementum annulations. We sexed, aged, weighed, measured, tattooed with a unique identifier, and equipped with a radiocollar (Advanced Telemetry Solutions, Isanti, Minnesota) and a microchip (AVID Co., Norco, California) every adult animal captured. We checked adult females for evidence of lactation during handling. We tattooed, microchipped, and released all kittens too small to wear a radiocollar. We conducted all procedures in accordance with Utah State University Institutional Animal Care and Use Committee standards (Approval No. 937-R).

We relocated all radio-collared cougars with the use of aerial and ground-based telemetry techniques (Mech 1983). We conducted telemetry flights bimonthly on both sites as weather conditions permitted. We also relocated cougars opportunistically with ground-based telemetry by plotting radiotriangulated locations on United States Geological Survey 7.5′ topographic quads with the use of Universal Transverse Mercator coordinates (zone 12, North American Datum 1927). We stored all locations in a Geographic Information Systems (GIS) database (ArcView, ESRI Products, Redlands, California).

Over the course of the study, radiocollared cougars on Monroe Mountain were not protected from harvest beyond normal legal stipulations outlined in the UDWR hunting proclamations. Annual hunter-kill was regulated by apportionment of a limited number of hunter permits, issued by the UDWR on the decision of the State Wildlife Board. The Camp Williams and Kennecott properties were closed to hunting throughout the study; however, radiocollared cougars leaving those properties were considered legal take on adjacent private and public lands within Unit 18 during the 1997–2001 hunting seasons. Radiocollared cougars on that unit were protected after 2002.

Demographic Parameters

Density.—We measured cougar density as the total number of adult and subadult cougars/100 km^2 present during winter. Our a priori goal was to capture and collar as many individuals as possible. In this sense, we attempted to conduct a census of the population during winter, but during no year were we able to capture all independent cougars. To derive a conservative estimate of the number of unmarked animals on the site, we used 2 methods. First, because males and females can generally be differentiated by track size (Fjelline and Mansfield 1989), we considered multiple track sets of same-sexed animals encountered in the same watershed one individual. Given the large ranges of cougars, we felt that the primary watersheds on the site ($n = 4$; mean ± SD = 361 ± 95 km^2, range = 237–462 km^2) provided a practical threshold for differentiating individuals, as these basins approximated the size of a male home range. This does not negate the possibility that some individuals were double-counted; however, the effect of this error on the population estimate was small due to the number of animals that fell into this category annually. Second, we back-calculated birthdates of radiocollared cougars from age estimations based on tooth wear and counts of cementum annulations and used this information to assess our estimates of uncollared individuals from track evidence and hunter harvest. We excluded males backdated in this manner from the population estimate when they were <3 years old because of the likelihood that they were recent immigrants. Because females tend to be philopatric (Sweanor et al. 2000), we included them in the population estimate as resident subadults at the backcalculated age of 1–2 years. Although there are exceptions to these arbitrary dispersal rules, they provide a reasonable cutoff point for population estimates based on known cougar behavior (Beier 1995, Sweanor et al. 2000). We summed the total number of animals detected (from all means: capture, deaths, tracks) in June at the end of the capture and hunting seasons. This number most accurately represented the population during the period June to December of the preceding year (Choate et al. 2006).

Road densities were high across both study areas. In addition to using 4-wheel-drive vehicles, we conducted winter tracking efforts on horseback and snowmachine in order to reduce bias associated with different levels of access. Using multiple methods also helped to reduce bias in terms of the social classes most vulnerable to detection due to frequent road crossings or small home ranges (Barnhurst 1986). Snow conditions influenced our ability to detect tracks, and therefore dry winters may have some bias associated with population counts; however, this bias was likely consistent between sites, as both study areas are subject to similar weather patterns.

We based study-area boundaries on major roads surrounding the site; therefore we used ecologically relevant vegetative and topographic features to delineate and quantify habitat within the study-site perimeter. We used the criteria of Laing and Lindzey (1991), which excluded valley bottoms and landcover types dominated by urban and agricultural uses. Maps represent geographical area on the planar surface and do not account for slope differences in mountainous terrain where actual surface area is greater. This discrepancy in area calculation leads to an increasing overestimation of population density as the ruggedness of the terrain increases. In order to increase the accuracy of the density estimates we used GIS software (ArcView surface to area ratio extension, Jenness Enterprises, Flagstaff, Arizona) to calculate the surface areas of habitat within study-site perimeters.

Age structure.—We determined age at the time of capture by visual inspection of tooth wear and gumline recession (Ashman et al. 1983, Laundré et al. 2000). In a few cases we used counts of cementum annulations (Matson's Lab, Milltown, Montana). To test for age differences among treatment groups (site and sex combinations), we used a 2-way factorial analysis of variance in a completely randomized design with unequal variances. We adjusted significance levels for pairwise mean comparisons to control experimentwise Type I error with the Tukey-Kramer method.

Cause-specific mortality.—We determined causes of mortality through visual inspection and necropsy of carcasses. When we could not determine cause of death in the field, we submitted the carcass to the Utah State University Veterinary Diagnostics Lab for detailed analysis. We calculated mortality by tallying cause of death among radiocollared animals and unmarked animals found opportunistically during tracking sequences. We pooled all human-related causes by site and tested for proportional differences with the use of chi-square (χ^2) tests.

Survival.—We calculated survival annually for all radiocollared adult and subadult animals from each population. To account for staggered entry and censoring due to the additions and losses of radiocollared animals to the sample, we used a Kaplan-Meier product limit estimator (Kaplan and Meier 1958). We estimated annual survival by defining the start of sample intervals as 1 December of each year. By beginning the sampling interval prior to the beginning of the hunting season (15 Dec), we ensured that human-related mortality is accounted for only once during a single nonoverlapping period in each year. We calculated measures of precision for the computed survival rates from procedures described by Cox and Oakes (1984; cited in Pollock et al. 1989). We compared survival curves between sites with the use of the log-rank test (Pollock et al. 1989).

Fecundity.—We measured fecundity as the proportion of sexually mature females detected with litters-of-the-year (kittens <1 yr) on site during winter. We counted litters during snow tracking and capture efforts. We checked all females taken in the hunt for signs of lactation, which helped account for otherwise undocumented reproduction. Kittens >3 months old are only found with their mothers 20–43% of the time (Barnhurst 1986), but we tracked many female cougars on multiple occasions, thereby increasing the probability of detecting kittens, if present. We did not attempt any analyses on the actual number of kittens born per litter, because of the difficulty in determining the actual number of kittens when ≥ 2 track sets were found. There are 2 potential sources of error in this estimate. First, it is possible that some maternal females experienced whole-litter loss prior to the winter tracking season, and therefore a proportion of nonlactating females or those without kittens may actually have been reproductively active that season. Second, kittens <2 months old are not mobile, and so this cohort would also have been missed through track-based counts. Consequently, both the number of kittens per litter and the proportion of reproductively active females are biased low. The minimum percentage of females caring for young provided an annual estimate of productivity for each population (Barnhurst 1986). We used paired t-tests to detect differences in mean fecundity rates pooled over the entire study interval.

Dispersal.—We tattooed the ears of all kittens handled on the Oquirrh mountain site in the event that they were recaptured as adults. For the Oquirrh Mountain animals, we were able to calculate several crude estimates of dispersal distance and direction opportunistically based on harvest returns of animals marked as kittens. In addition, we monitored subadults captured as transients on Monroe via radiotelemetry for extrasite movements, thus providing some information on coarse-scale movement patterns. We calculated distances as a straight line between capture site and death site or the center of the home range.

Landscape Configuration

We used measures of landscape configuration to assess the overall degree of connectivity of the study sites to surrounding habitats within their respective ecoregions. Connectivity is defined here as "the degree to which the landscape facilitates or impedes [animal] movement among resource patches" (Taylor et al. 1993). We used descriptions provided by Laing and Lindzey (1991) to delineate potential connective habitats between the study areas and neighboring patches. In assessing connectivity for cougars we used only easily quantifiable landscape variables and did not consider potential psychological barriers, although there is some evidence that outdoor lighting may function as such (Beier 1995). We derived the following metrics: size (km^2), shape (perimeter–area ratios), greatest interpatch distance, percent of perimeter connected to neighboring habitat patches, width of connective habitat, and percent of perimeter impermeable to cougar movement. Impermeability refers to landscape features that prohibited, filtered, or redirected animal movement (Ernest et al. 2003, Forman et al. 2003), such as the Great Salt Lake, interstate highways, and urban areas. Some of these features may not form absolute barriers, but they can act as an impediment to animal movement. Perimeter-area ratios are a unitless metric that provided a relative measure of how circular (or how much edge) one study area had relative to the other. We derived these measures in ArcView using the spatial analyst extension and a 30-m digital elevation model of the state of Utah.

Results

Radiotelemetry and Harvest

Capture.—We captured and marked 110 individual cougars on the 2 study sites, representing 145 capture events (Table 1). In addition, we found one dead cougar opportunistically during tracking on the Oquirrh site. We conducted captures on Monroe Mountain from January 1996 to March 2004 and on the Oquirrh site from February 1997 to March 2004. Rugged terrain and frequent animal use of culverts, mine shafts, and lava tubes hindered the collection of ground-based telemetry observations. Consequently most telemetry data were derived from aerial surveys. Monitoring times for Monroe cougars averaged 758 days (range = 2–3140 days) for females, and 194 days (range = 3–662 days) for males. On the Oquirrh site we monitored females for a mean of 810 days (range = 14–2674 days) and males for 399 days (range = 76–1173 days). Differences between sexes reflected the smaller sample of males, their greater tendency to emigrate, and shorter residence times.

Monroe Mountain cougar harvest.—For the period 1990–1995, prior to initiation of this study, a mean of 15.6 (range = 14–19) hunting permits were issued annually, corresponding to a mean kill of 8.7 cougars per year (range = 6–12), and a mean hunter success of 54.0% (range = 40.7–64.9%). In 1996, the number of permits issued increased 33.7% over the 1990–1995 mean. In 1997, the number of permits increased 40% over 1996 levels and 151% over the 1990–1995 mean. Between 1999 and 2000, the number of permits issued decreased to 1990–1995 mean levels and was again decreased for the 2001 season. During the years of heavy harvest (1996–2001), mean per-capita hunting pressure (i.e., the proportion of the population that was legally harvestable) was 87% (range = 68.5–100%). During the years of reduced harvest (2002–2004) mean per-capita hunting pressure was 25.7% (range = 22.7–29.4%; Table 2). During the study 164 permits were issued, 79 cougars were killed (51 M, 28 F), and total hunter success was 48.1%, whereas mean annual hunter success was 46.5% (1996–2001) and 73.3% (2002–2004; Hill and Bunnell 2005). The general decline in the number of hunting tags issued over time was partially in response to preliminary study results.

Table 1. Number of cougars captured according to age and sex classes, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Age and sex	Monroe	Oquirrhs
Adults		
F	16	20
M	12	7
Subadults		
F	14	2
M	15	3
Kittens		
F	2	9
M	1	9
Totals	60	50

Oquirrh Mountain cougar harvest.—From 1996 to 2001 radiocollared animals on Unit 18 were considered legally harvestable. Cougars on the Camp Williams and Kennecott properties were protected, but these areas were surrounded by private and public lands open to hunting, making any study animal found offsite legal quarry. Beginning in 2002, all radiocollared animals on the unit were protected by law regardless of property ownership to facilitate a concurrent study. During our study 5 radiocollared cougars were killed just outside the study site boundaries (4 M, 1 F). Of these, the 4 males were legally harvested, whereas the female was taken after the 2002 moratorium on radiocollared study animals.

Demographic Parameters

Density.—Estimated high densities (cougars/100 km^2) were similar between sites (Oquirrhs, 2.9; Monroe, 3.2); however, trends in this parameter differed markedly (Fig. 2). Density on Monroe showed a consistent decline during the years of heavy harvest (1997–2001), which leveled off when permits were reduced by 80%, averaging 2.0 ± 0.3 (2002–2004). Oquirrh density showed minimal variation over the study interval averaging 2.8 ± 0.1 (Fig. 2).

Age structure.—Age estimates determined upon initial capture were pooled by sex and site for the entire study period (Table 1). Sexually mature cougars from the Monroe population ($n = 57$) averaged 3.4 ± 0.2 years (F = 3.7 ± 0.4; M = 3.1 ± 0.3). Adult cougars from the Oquirrh population ($n = 33$) averaged 4.6 ± 0.3 years (F = 5.9 ± 0.5; M = 3.4 ± 0.4; Fig. 3). Mean cougar ages differed both by study site (Monroe cougars < Oquirrh cougars; $F = 9.0$, df = 1,60.3, $P = 0.004$) and by sex (F > M; $F = 13.8$; df = 1, 60.3; $P < 0.001$). Further, we found evidence of an interaction between sex and site ($F = 5.31$; df = 1, 60.3; $P = 0.025$). Within the Monroe population male and female mean ages did not differ ($t = 1.21$; df = 54.6; $P = 0.625$), whereas Oquirrh females were significantly older than their male counterparts ($t = 3.70$; df = 30.2; $P = 0.003$). Between sites, Oquirrh females were older than Monroe females ($t =$

Table 2. Cougar harvest characteristics from Monroe Mountain (Unit 23), Utah, USA, 1996–2004.

Hunting season	Estimated population[a]	Permits issued	Cougars killed[b]	% hunter success	% F	% population Hunted[c]	% population Killed
1995–96	35	24	14	58.3	42.9	68.5	40.0
1996–97	42	40	17	42.5	47.1	95.2	40.5
1997–98	33	30	15	50.0	26.7	90.9	45.5
1998–99	26	25	7	28.0	28.6	96.1	26.9
1999–00	21	15	9	60.0	44.4	71.4	42.9
2000–01	15	15	6	40.0	33.3	100.0	40.0
2001–02	17	5	3	60.0	33.3	29.4	17.6
2002–03	20	5	4	80.0	00.0	25.0	20.0
2003–04	22	5	4	80.0	25.0	22.7	18.2
Mean	25.6	18.2	8.8	55.4	31.2	66.6	32.4
SE	3.0	4.1	1.8	17.5	5.0	10.8	3.8

[a] Estimated number of adults and independent subadults from winter capture and tracking efforts.

[b] Legal sport harvest only (Hill and Bunnell 2005).

[c] Per capita hunting pressure, i.e., the ratio of the number of permits issued to the estimated population size (column 3/column 2).

-3.53; df $= 38.8$; $P = 0.004$), but male ages did not differ between sites ($t = -0.54$; df $= 22.5$; $P = 0.949$).

Cause-specific mortality.—Mortality on the Monroe site was predominantly human caused (74%), with legal harvest accounting for 81% of human-caused ($n = 26$) and 60% of total mortality ($n = 35$) (Fig. 4). Causes of mortality on the Oquirrh site varied (Fig. 4). All human causes (including roadkill) comprised 53% of the total mortality ($n = 17$) and of this, legal harvest accounted for 44% of all human-caused mortality ($n = 9$) but only 24% of the total. Levels of human-caused mortality differed between sites ($\chi^2 = 7.5$; $P = 0.006$). Various forms of poaching (neck snares, illegal hunter-kill) occurred sporadically on both sites (Monroe, $n = 2$; Oquirrhs, $n = 1$), though alone, this did not represent a significant source of mortality for radio-collared animals.

The second leading cause of death on both sites was intraspecific predation, comprising 17% ($n = 6$) and 18% ($n = 3$) of total mortality on the Monroe and Oquirrh sites, respectively. During the years of high per-capita harvest pressure on Monroe, all victims of intraspecific aggression were resident adult females ($n = 4$), whereas during the period of light harvest all victims were subadult males ($n = 2$). On the Oquirrhs, 1 victim was a predispersal subadult male and 2 were adult females. Notably, one of these instances was an adult female cannibalizing another female with dependent young. Two years later, the survivor in this encounter was killed by an unidentified cougar. Cause of death could not be determined in three cases (2 F, 1 M), but did not appear to be human-related.

In addition to direct mortality, ≥11 kittens from 5 different litters on Monroe were orphaned when their mothers were killed during the winter hunt ($n = 10$) or during summer depredation control actions ($n = 1$). We confirmed the death of one orphaned litter (2 kittens, approx. 6 months old) due to dehydration and malnutrition. On the Oquirrhs, one male kitten was orphaned at the estimated age of 9 months when its mother was killed by an automobile. This animal survived 6 weeks before being taken in a depredation control action on a small ranch just outside of Salt Lake City. A litter of 3 4-month-old kittens died following the disease-related death of their mother. One other male kitten was marked at the age of 7 months following the poaching-related death of its mother in January 2002. It survived at least 2 months before radio contact was lost. Aside from this individual, no other orphans were detected following the deaths of their mothers or as adults on either study area in subsequent years.

Survival.—Adult survival varied between sites and among years (Fig. 5). On Monroe, survival tracked harvest

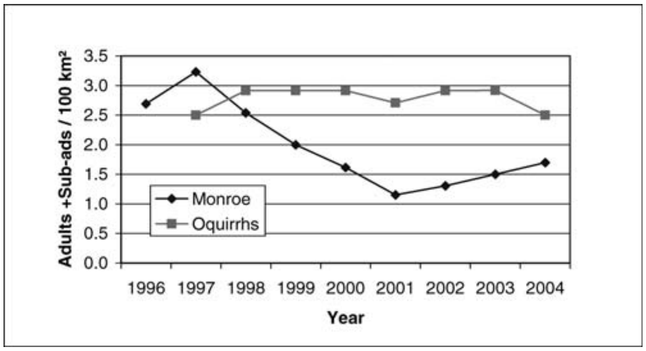

Figure 2. Annual nonjuvenile cougar density as determined from capture, tracking, and harvest, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

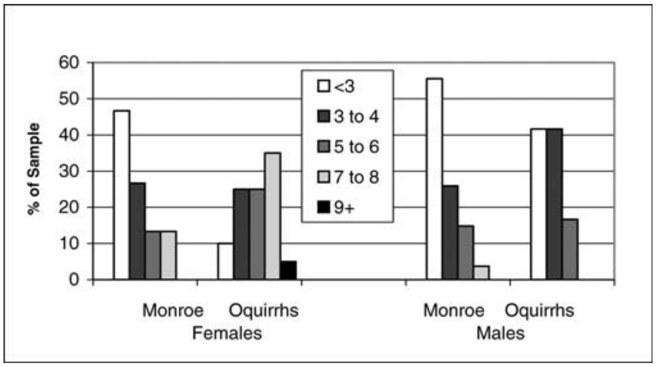

Figure 3. Age distribution of radiocollared cougars by sex, Monroe ($n = 57$) and Oquirrh ($n = 30$) Mountain study sites, Utah, USA, 1996–2004.

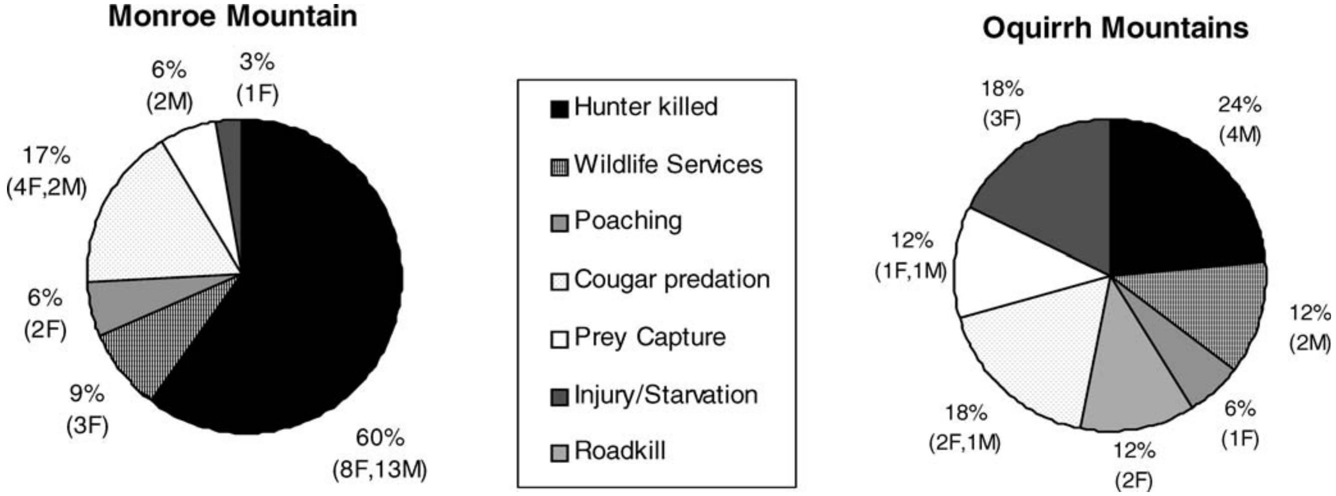

Figure 4. Cause-specific mortality among radiocollared cougars from the Monroe ($n = 35$) and Oquirrh Mountain ($n = 17$), study sites, Utah, USA, 1996–2004.

intensity, ranging from a high of 1.0 in 1996, just prior to the initiation of the treatment period, and declining to a low of 0.36 ± 0.33 (95% CI) in 2001, the end of high per-capita hunting pressure. Survival on the Oquirrhs showed moderate variation, ranging from 0.63 ± 0.28 to 0.91 ± 0.17. Trends in survival mirrored those of density on both sites, averaging 0.64 ± 0.07 (± SE) on Monroe and 0.76 ± 0.04 on the Oquirrhs. Analysis of trends over the entire interval suggested a difference in survival between sites ($\chi^2 = 3.41$; df = 1, $P = 0.068$).

Fecundity.—Reproduction varied between sites and years (Fig. 6). The number of litters detected annually ranged from 0–9 on Monroe and from 1–5 on the Oquirrhs, averaging 0.24 ± 0.04 (Monroe) and 0.34 ± 0.05 (Oquirrhs) litters per sexually mature female. Although rates did not differ statistically between sites ($t = -1.23$; df = 7; $P = 0.258$), fecundity on Monroe tracked the population decline and included a zero detection rate in 2002, the year following the lowest population estimate. At that time there were ≥ 5 sexually mature females present. The lowest fecundity estimate for the Oquirrh population was recorded the year after a 50% reduction in elk numbers. These animals were removed for reintroductions in other states. The removal was conducted over 2 years and was comprised primarily of cows and calves, the sex and age classes most vulnerable to cougar predation (Murphy 1998). The number of resident females on the Oquirrh site was smaller ($\bar{x} = 9.6$/yr) than on Monroe ($\bar{x} = 15.7$/yr), which may have influenced the variability in fecundity. Litter sizes averaged 1.7 and 1.9 kittens per litter on Monroe and the Oquirrhs, respectively. Based exclusively on the Oquirrh site using only kittens handled and marked (4–10 months post partum), the sex ratio was even (9 F, 9 M).

Dispersal.—Several animals were captured and marked either just prior to, or during dispersal. Four cougars (1 F, 3 M) moved from Monroe to neighboring mountain ranges 19–55 km distant. Two of these (1 F, 1 M) established residency in habitat adjacent to the study area; one was recaptured and his collar removed (fate unknown); and one was harvested 42 km northeast on the Fishlake Plateau (Fig. 7).

Seven dispersals were documented on the Oquirrh site (2 F, 5 M), ranging in distance from 13 to 85 km (Fig. 7). Of these, 3 (1 F, 2 M) settled elsewhere in the Oquirrh Mountains; 1 female moved to the Simpson-Sheeprock Mountains; 2 males moved to the Stansbury Mountains where they were hunter-killed as transients; and 1 male dispersed to the Mt. Timpanogos region of the southern

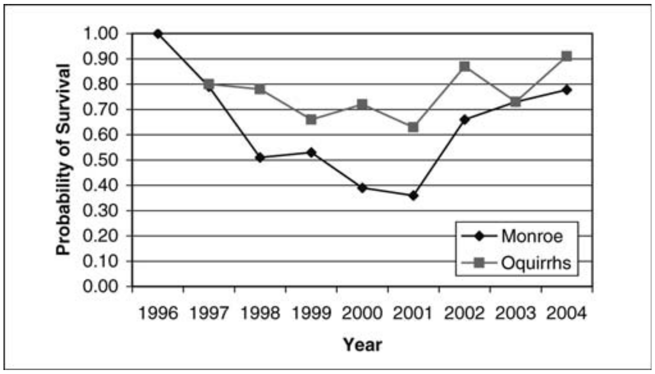

Figure 5. Estimated annual survival rates for radiocollared cougars, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

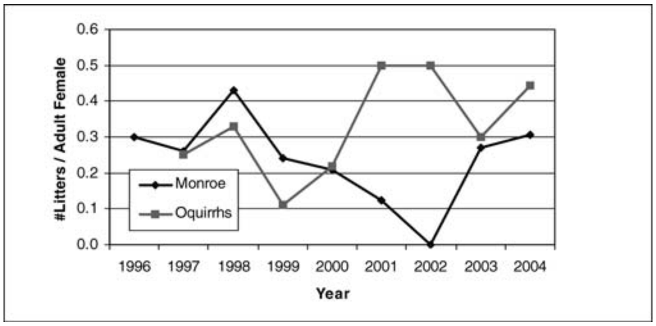

Figure 6. Annual fecundity rates for adult cougars on the Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

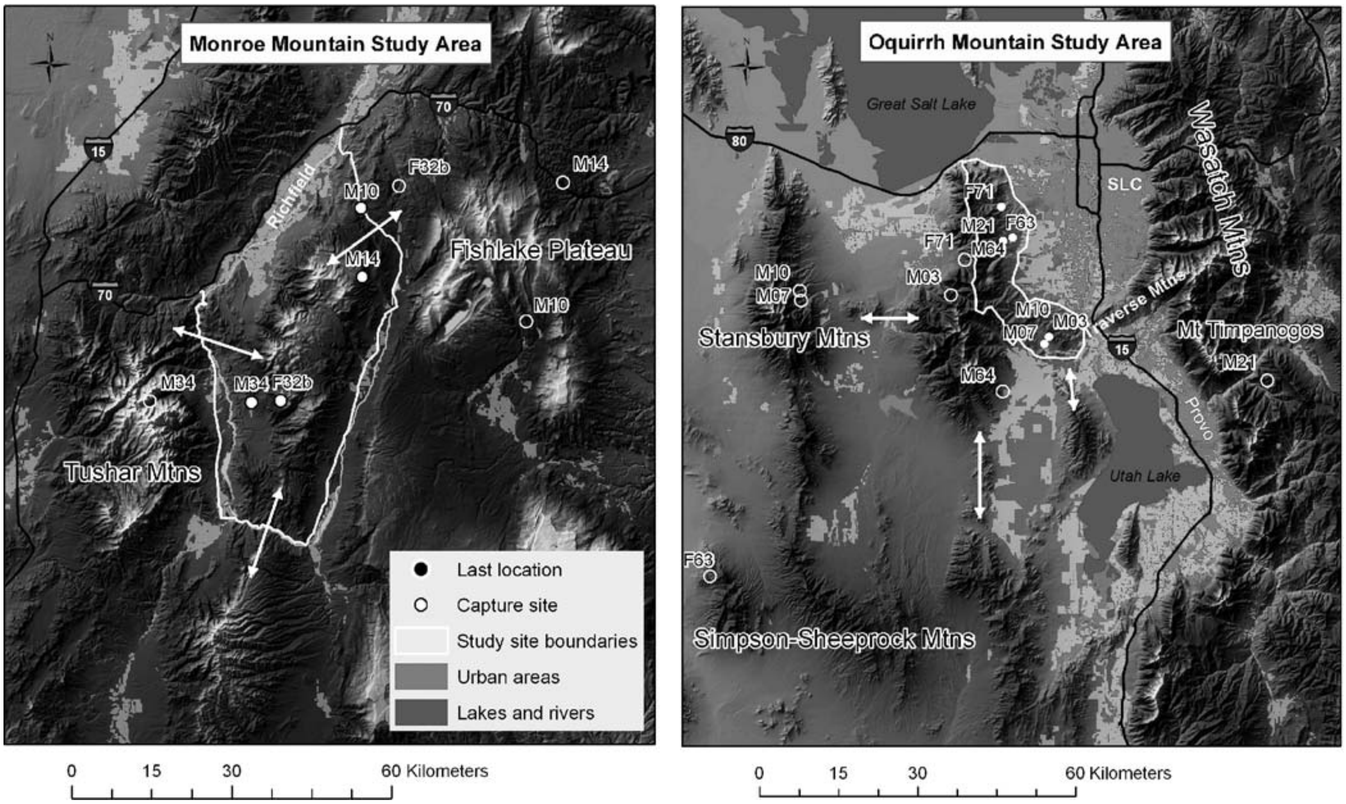

Figure 7. Dispersal patterns and landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004. Arrows represent points of habitat connectivity.

Wasatch Mountains, crossing a 6-lane interstate and ≥5 km of city streets to get there.

Landscape Configuration

The study sites exhibited similar perimeter-area indices, but notable differences in connectivity and perimeter permeability (Table 3). During the study, no substantial movement barriers existed along the perimeter of Monroe Mountain, and in general, the unit was well connected to other habitats of similar quality within the Southern Mountains ecoregion (Fig. 7).

In contrast, only 5% of the Oquirrhs' perimeter was connected to neighboring habitat and approximately 40% was nearly impermeable to cougar movement. Movement barriers included the southern shore of the Great Salt Lake (7 km), the Salt Lake metro area (50 km), and a heavily traveled segment of Interstate 15 (2 km), which bisected the Traverse Mountains (Fig. 7). The remaining 55% graded into salt desert scrub communities offering little vegetative cover or surface water (West 1983). Additionally, residential development emanating from the Salt Lake–Provo metropolitan corridor was much greater around the Oquirrh site.

Overall, the Oquirrhs exhibited much thinner and more tenuous connectivity to neighboring patches of generally poorer quality (i.e., lower primary production), a pattern typical of basin and range topography (Fig. 1). This topographic fragmentation combined with anthropogenic fragmentation in the foothills and valleys around the site rendered this area susceptible to isolation (see Beier 1995).

Discussion

Influence of Harvest on Cougar Populations

Demographic differences between study populations reflected the prevailing management strategies. Cougar removal on Monroe Mountain ranged from 17.6–54.5% of the adult population exceeding 40% for 4 of the 5 years of high per-capita hunting pressure. Females comprised 32% of the harvest but 100% of depredation control and poaching mortality. Under this regime the population declined by >60%, whereas the Oquirrh Mountain population remained stationary. Moreover, the Oquirrh population had a significantly higher mean age among females and a smaller proportion of subadults. Age structure of males did not differ between sites, suggesting either: 1) males and females had a fundamentally different age distribution in the general population, or 2) the unhunted portion of the Oquirrhs was too small to adequately protect males. Density, survival, and fecundity were all negatively associated with sustained high per-capita hunting pressure on Monroe Mountain, whereas, with the exception of fecundity, these measures remained relatively constant over the same interval on the Oquirrh site. Though humans represented the single greatest source of mortality for animals traveling outside the Oquirrh study site, the absence of harvest within the study area suggests that the Camp Williams–Kennecott properties collectively acted as a functional refuge. Resident females were the primary beneficiaries of this protection. On the Monroe site, the prevalence

Table 3. Measures of landscape connectivity, Monroe and Oquirrh Mountain study sites, Utah, USA, 1996–2004.

Landscape metrics	Monroe	Oquirrhs
Perimeter (km)	178	150
Area (km^2)	1300	950
Perimeter:area	0.137	0.157
Greatest interpatch distance (km)	7	25
Perimeter impermeable (%)	0	40
Perimeter connected (%)	33	5
Width connective habitat (km)	7–21	2–4.5

of human-caused mortality, lack of starvation as a mortality cause, and moderately stable prey populations (UDWR, unpublished data) suggest that this level of mortality was largely additive. Annual harvests exceeding 30% of the adult population consisting of 42% females, carried out continuously for >3 years, can reduce density, fecundity, and skew age structure.

The consequences of sustained exploitation may not be limited to numeric population changes. Fecundity rates on Monroe tracked per-capita harvest pressure with a 1-year lag. We did not observe compensatory reproduction under increased harvest levels, as has been noted for some monogamous carnivores (Knowlton 1972, Frank and Woodroffe 2001). Smuts (1978), Knick (1990), and Wielgus and Bunnell (2000) reported analogous findings for hunted populations of African lions (*Panthera leo*), bobcats (*Lynx rufus*), and brown bears (*Ursus arctos*), respectively. One hypothesized function of male territoriality among polygynous carnivores is to increase offspring survival by excluding nonsire males from the natal range (Bertram 1975, Ross and Jalkotzy 1992), thereby reducing infanticide and optimizing fitness (Packer and Pusey 1984, Swenson 2003). Cougars are known to exhibit this behavior (Hornocker 1970, Hemker et al. 1986, Pierce et al. 1998) suggesting that hunted populations may experience increased levels of infanticide (Swenson 2003). On Monroe heavy harvest and subsequent social instability may have reduced the reproductive capacity of the population and therefore its ability to compensate losses.

Factors Influencing the Rate of Population Recovery

From 2002 to 2004 per capita hunting pressure on Monroe Mountain was reduced to <30%, during which survival and fecundity increased. Nevertheless, following 3 seasons of light harvest the population had only recovered to 52.4% of its 1997 levels, with nearly equal sex ratios and reproduction lagging behind resident replacement.

Lindzey et al. (1992) in Utah and Logan and Sweanor (2001) in New Mexico conducted controlled removals to examine the demographic mechanisms and time scales of population recovery. These authors noted that female recruitment was achieved via philopatric behavior or diffuse dispersal, whereas male recruitment was solely the product of immigration. Further, they suggested that recovery from 27–58% population reductions could be attained within 2–3 years under complete protection. However, those removals spanned only a single season and large sanctuaries (>1,000 km^2) buffered the treatment areas. In contrast, the Monroe population had only a 7-month annual reprieve from hunting pressure and was surrounded by units subjected to similar levels of exploitation.

The degree of landscape connectivity can mediate demographic connectivity, and is thus an important factor in population recovery or persistence (Beier 1993). Strong connectivity is the most likely reason we detected transients on Monroe each winter. These animals buffered population declines (Brown and Kodric-Brown 1977) but may have contributed to social instability. It has been hypothesized that the removal of resident males may induce a "vacuum effect" in which multiple transients vie for a vacant home range, potentially leading to an increase in population density (Shaw 1981, Logan et al. 1986). Our results lend only limited support to this argument. We observed an increase in the relative proportion of subadult males subsequent to removal of resident males, whereas the overall population declined. In general, males tend to disperse farther than females, remain transient longer, and are less tolerant of other males (Cunningham et al. 2001, Logan and Sweanor 2001, Maehr et al. 2002). Conversely, females often exhibit philopatric behavior, reproduce at an earlier age than males, and tolerate spatial overlap with other females (Murphy 1998, Pierce et al. 2000). Therefore, the transient segment of the cougar population is likely to be male biased (Hansson 1991). Removal of resident males provides territory vacancies that may be contested by multiple immigrants, thereby temporarily increasing the proportion of males in the population but not the overall density of males in the general population. Based on preliminary data from the post-treatment period, we hypothesize that following sustained disturbance, population recovery will proceed in 2 general phases: numerical and functional. Functional recovery implies not simply increases in absolute density but rather stabilization of social relationships and decreases in the variability of vital life-history rates. Female-biased sex ratios, low male turnover rates, and higher per-capita productivity may be used as relative indices of functional recovery.

Harvest Dynamics and the Regional Metapopulation

The metapopulation concept has been proposed as a framework for large-scale management of cougars (Beier 1996, Sweanor et al. 2000, Laundré and Clark 2003). In the strictest sense, a metapopulation is the composite of numerous spatially discrete subpopulations exhibiting independent behavior over time. The dynamics of the metapopulation are the net result of the shifting balance between local extinctions and recolonizations facilitated by intermittent dispersal events. The latter quality defines the classic metapopulation (Levins 1969, Hanski and Simberloff 1997).

The source–sink model provides a mechanism for metapopulation dynamics by emphasizing recruitment patterns within and among populations. The more general definition describes a sink as a net importer and a source as a net exporter of individuals over time (Pulliam 1988). Demographically, the Monroe and Oquirrh populations approximate the sink–source archetypes, respectively, albeit as a result of exploitation levels rather than habitat quality (e.g., Novaro et al. 2000). When harvest and its apparent impacts are considered, the Monroe population exhibited sink-like mortality. Notwithstanding low kitten production, each winter new animals, primarily subadult males, were captured on the site. Some of these individuals may have been resident progeny but mammalian dispersal patterns tend to be male-biased (Greenwood 1980). Low productivity and high immigration rates are the essence of a sink population.

In contrast, the Oquirrh population exhibited static density and emigration of resident progeny. No marked female kittens were detected as adults on the site. Indeed, 5 tattooed kittens (2 F, 3 M) were later killed elsewhere in the Oquirrhs or on neighboring mountain ranges up to 85 km distant. Solely based on age (4 yr) the female emigrants could have raised one litter to independence, whereas the males were killed immediately upon leaving their natal ranges, thereby subsidizing the harvest in adjacent units. On the Oquirrh site female dispersal appeared to be related to the saturation of available habitat, suggesting a source-like population structure.

When the prevailing harvest rate is considered a component of habitat quality, then a spatially clumped harvest distribution can promote source–sink dynamics. This may result in an immigration gradient directed toward patches such as Monroe Mountain, where strong connectivity coupled with low population density create an ecological trap (i.e., a productive habitat that displays sink-like mortality patterns, e.g., Bailey et al. 1986, Kokko and Sutherland 2001). These sites represent examples of populations exhibiting different dynamics simultaneously within a metapopulation. Importantly, source–sink characteristics may be dynamic and interchangeable depending on how prevailing management interacts with habitat productivity and connectivity. For example, the Monroe population illustrates the potential consequences of overharvest, yet is situated within a large semicontiguous tract of habitat spanning the state with extensions into Colorado, Idaho, and Arizona. Conversely, the Oquirrh population appears demographically stable, but lies within an ecoregion defined by weak connectivity among sparsely distributed desert ranges. Under different objectives, conservative management could render the Monroe population a source, whereas the Oquirrh population should be managed under the small population paradigm (Caughley 1994).

Management Implications

At the scale of the local population or management unit, annual harvests exceeding 40% of the nonjuvenile population for $\geq$4 years can not only reduce density but may also promote or maintain a demographic structure that is younger, less productive, and socially unstable. At an ecoregional scale the difficulties of reliably delineating discrete populations (Pierce and Bleich 2003) and their respective sizes (Choate et al. 2006) emphasize the importance of managing cougars in a metapopulation context. That said, source–sink characteristics may be more amenable to field evaluation than the extinction and recolonization events that define classic metapopulations. Numeric recovery of overexploited populations may initially depend more on immigration than in situ reproduction. Under moderate to heavy exploitation this tack may require: 1) an assessment of habitat connectivity between identified sources and sinks, and 2) the presence of truly functional source populations, most readily managed through the establishment of refugia.

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REVIEW

Hunting for large carnivore conservation

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Summary

1. Carnivores are difficult to conserve because of direct and indirect competition with people. Public hunts are increasingly proposed to support carnivore conservation. This article reviews scientific evidence for the effectiveness of public hunts of large carnivores in attaining three common policy goals: stable carnivore populations, preventing conflict with carnivores (property damage and competition over game) and building public support for carnivore conservation.

2. Sustainable exploitation of stable wildlife populations has a solid, scientific foundation but the theory and its predictions must be adapted to complex patterns of carnivore behavioural ecology and population dynamics that demand years of landscape-level monitoring to understand fully.

3. A review of the evidence that hunting prevents property damage or reduces competition for game reveals large gaps in our understanding. Reducing the number of large carnivores to protect hunters' quarry species seems straightforward but we still know little about behavioural and ecological responses of the contested prey and sympatric meso-predators. For reducing property damage, the direct effect – numerical reduction in problematic individual carnivores – presents numerous obstacles, whereas the indirect effect – behavioural avoidance of humans by hunted carnivores – holds more promise.

4. Scientific measures of public support for carnivore-hunting policies are almost completely lacking, particularly measures of attitudes among hunters before and after controversial wildlife is designated as legal game species. Moreover, illegal killing of carnivores does not appear to diminish if they are designated as game.

5. *Synthesis and applications*. Sustainable hunting to maintain stable populations is well understood in theory but complex life histories of carnivores, and behavioural changes of hunters and the carnivores they stalk may result in unsustainable mortality for carnivores. The direct impact of hunting on carnivore damage to property is unclear and even doubtful given the inability or unwillingness of hunters to remove specific individuals selectively. However, hunters may indirectly deter carnivores from people and their property. The assumption that hunters will steward carnivores simply because they have in the past helped conserve other game species requires more study as preliminary results suggest it is incorrect. Policy-makers may achieve support for policy if they mesh utilitarian and preservationist values held by the general public. A number of opposed hypotheses should be disentangled before researchers confidently inform policy on sustainable hunting to prevent conflicts and build public support for carnivore conservation.

Key-words: animal damage management, attitudes, conflict, harvest, lethal control, wildlife policy

Introduction

Bears, big cats, wild canids and other large carnivores are difficult to live alongside and pose particular challenges for conservation. Two species – Malvinas 'wolf' *Dusicyon australis* and Tasmanian 'wolf' *Thylacinus cynocephalus* – have gone extinct in recent times and most others have suffered major population reductions (Ray, Hunter & Zigouris 2005; Sillero-Zubiri, Sukumar & Treves 2007). The loss of large carnivores has cascading influences on lower trophic levels, smaller-bodied

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carnivores and vegetation dynamics (Terborgh *et al.* 2002; Ripple & Beschta 2004). The larger carnivore species typically require vast areas to survive, thereby competing indirectly with people for space and resources. Direct competition is also apparent as people cause most mortality of virtually every large carnivore population (Woodroffe & Ginsburg 1998; Andren *et al.* 2006; Adams *et al.* 2008; Obbard & Howe 2008; Robinson *et al.* 2008).

People mainly retaliate against carnivores for real and perceived threats to property, safety or game species (Marker *et al.* 2003; Treves & Naughton-Treves 2005; Woodroffe & Frank 2005). Both private citizens and governments are implicated. Government-sponsored bounties, pest eradication campaigns and trophy hunts extirpated carnivores across vast areas of many countries (McDougal 1987; Treves & Naughton-Treves 1999; Knight 2003; Riley, Nesslage & Maurer 2004). Local, private eradication also took place in the last decade (Karanth & Madhusudan 2002; Treves & Naughton-Treves 2005). Hence, carnivore conservation efforts often focus on reducing human causes of mortality.

Despite this history, a number of regions are considering reopening or expanding public hunting of carnivores. Public hunts are touted for many reasons in many countries: revenue, trophies and animal products, recreation, population control, property protection, etc. (Wilkie & Carpenter 1999; Mincher 2002; Bartel & Brunson 2003; Heberlein 2008; Campbell & Mackay 2009). Counter-arguments are also numerous and widespread on ethical, functional and economic grounds (Rutberg 2001; Knight 2003; Peterson 2004; Campbell & Mackay 2009). For example, US interest groups often clash over proposals to hunt grey wolves *Canis lupus* (Harbo & Dean 1983; Treves 2008). Thus, policy-makers face clear challenges in designing politically acceptable hunting of large carnivores. Here, I review scientific evidence on the effectiveness of public hunting of large carnivores to attain three common policy goals: (i) To maintain populations at target levels (maintain stable population); (ii) To reduce conflicts over property including competition with human hunters who claim ownership of their game (reduce conflicts) and (iii) To build political support for carnivore conservation (build public support).

This review is intended to outline gaps in knowledge, suggest tests of hypotheses and consolidate information for policy-makers. I present conjectured advantages and disadvantages as opposing hypotheses (Table 1). I do not address other goals of carnivore hunts, such as revenue, recreation or extraction. These are less common as policy goals although the second and third goals clearly motivate some hunters.

HUNTING CARNIVORES TO MAINTAIN POPULATIONS AT TARGET LEVELS (MAINTAIN STABLE POPULATION)

Theory relating wildlife population dynamics to sustainable mortality rates is mature and well supported (Keith 1983; Groom, Meffe & Carroll 2007; Person & Russell 2008). In practice, many governments have regulated public hunting to control carnivore populations for decades (Okarma 1993; Logan & Sweanor 2001; Adams *et al.* 2008; Obbard & Howe 2008). Yet, carnivore researchers continue to refine the theory and undermine simplistic assumptions about the effects of hunting, as they discover unsustainable mortality under many conditions. For example, hunting of trophy male lions *Panthera leo* remains contentious because of complex variation in male reproductive success relating to age, coalition size and pride residence length (Whitman *et al.* 2004; Loveridge, Reynolds & Milner-Gulland 2007a; Loveridge *et al.* 2007b). Refinements to theory also come from long-term studies of wolf and cougar *Puma concolor* movements within and between hunted populations, which undermine assumptions about closed populations or balanced in- and out-migration (Adams *et al.* 2008; Person & Russell 2008; Robinson *et al.* 2008). Concern has also risen over undetected mortality following removal of breeding adults, as dependent young starve or fall victim to newcomers filling vacancies (Czetwertynski, Boyce & Schmiegelow 2007; Garrison, Mccown & Oli 2007; Obbard & Howe 2008; Balme *et al.* in press). Thus, the successful design of hunting to maintain stable large carnivore populations is seldom simple and straightforward.

There is also an unresolved debate about the need for hunting to limit carnivore population growth. Some would argue that carnivores limit their own population densities below a

Table 1. Summary of hypotheses about public hunting of carnivores to attain three goals

Goal	Hypothesized advantages	Hypothesized disadvantages
Maintain stable population	Well understood and responsive to carnivore population fluctuations Generates revenue and data for scientific management	Promotes volatility if migration rates are high and variable Promotes unsustainable mortality if monitoring is inadequate or regulators profit from hunting Adds to other sources of mortality to become unsustainable Drains nearby protected areas
Reduce conflict	Reduces numbers of 'problem' animals Survivors avoid humans and their property	Removes uninvolved animals Exacerbates carnivore damage by displacement, injury, or social disruption
Build public support for carnivore conservation	Elevates the value of carnivores as game so hunters steward them Reduces carnivore mortality from illicit killing	Non-hunters will oppose carnivore-hunting policy and management

level that would alter or deplete ecosystems (except perhaps on islands) – more so than wildlife at lower trophic levels, which can reach densities that degrade ecosystems (Ripple & Beschta 2004; Rooney & Anderson 2009; Vucetich & Peterson 2009). The density-dependent factors regulating carnivore populations that are most often cited include intraspecific aggression and indirect (scramble) competition for resources. However, others would argue that hunting can prevent carnivores from colonizing areas where they are undesirable to people, or can lower densities so that undesirable behaviour is minimized, e.g. competition with hunters for game (Conover 2001; Herfindal *et al.* 2005; Hristienko & McDonald 2007).

The behaviour of people and carnivores compound the complexities mentioned above. Participation in hunting seasons varies with political conditions producing unexpected volatility in carnivore populations or failure of agency plans. Military action may reduce hunter availability and political clashes between hunters and managers may dampen enthusiasm for proposed hunts (Okarma 1993; Heberlein 2004). Also carnivores alter their behaviour to avoid people or their haunts, especially during the hunting season (Diefenbach *et al.* 2005; Bunnefeld *et al.* 2006; Person & Russell 2008). The mere presence of hunters pursuing other prey can affect carnivore behaviour. For example, a small sample of grizzly bears *Ursus arctos* made forays out of Yellowstone National Park, USA, at the start of the public, ungulate hunting season, whereas cougars did the opposite and wolves showed variable responses (Ruth *et al.* 2003).

Faced with dynamic behavioural and population ecology of carnivores, managers of public hunting may have to invest heavily in monitoring and data analysis or set highly conservative, precautionary quotas (Person & Russell 2008). Inadequate monitoring can mask unsustainable mortality in several ways. For example, using past hunting success to set future quotas can lead to unsustainable off-take (Logan & Sweanor 2001). Hunting in a small area can subtly drain nearby protected populations (Woodroffe & Ginsburg 1998; Loveridge *et al.* 2007a,b). Adding to honest mistakes, the quest for profit may motivate over-hunting (Wilkie & Carpenter 1999; Rutberg 2001; Loveridge *et al.* 2007a,b). High investment in monitoring may reduce the net profits from a hunt, but may gain the support of scientists funded by the money generated. Hunting for the wrong reasons can alienate other constituencies (Campbell & Mackay 2009; A. Treves & K.A. Martin, unpublished data 2009).

Research continues to improve our understanding of sustainable mortality in species with complex social systems and large-scale movement patterns. By contrast, scientific understanding of behaviour and cost-effective monitoring is less well developed. I include in these gaps both hunter behaviour and the effects of hunters on carnivore behaviour.

HUNTING CARNIVORES TO REDUCE CONFLICTS OVER PROPERTY INCLUDING COMPETITION WITH HUMAN HUNTERS WHO CLAIM OWNERSHIP OF THEIR GAME (REDUCE CONFLICT)

Governments have shown they can eradicate carnivores and thereby prevent property damage (Newby & Brown 1958; Treves & Naughton-Treves 1999; Woodroffe 2000; Riley *et al.* 2004), but public hunting to prevent property damage and simultaneously to conserve carnivore populations remains an uncertain approach. Governments and advocates often hope it will work (Mincher 2002; Bartel & Brunson 2003; Hristienko & McDonald 2007). For example, the chief legal counsel for Montana Fish Wildlife & Parks said his state 'could preserve its wolf population indefinitely while still using hunts to deal with wolves that kill livestock' (Brown 2008). Accordingly, hunting quotas have been set in part according to past damage (Jorgensen *et al.* 1978; Sunde, Overskaug & Kvam 1998; Huygens *et al.* 2004), or lifted entirely in agricultural areas (Garshelis 1989), but systematic study raises doubts about the underlying assumptions of these policies.

One basic assumption is that large carnivores taken by hunters would otherwise damage property or compete for game (Conover 2001; Bartel & Brunson 2003). This assumption is most accurate when the property is an important resource on which the carnivores evolved specializations. For example, if humans claim a staple, wild food as their property, any carnivore would be in conflict. There is an ample scientific literature on small to medium-sized predator control, including hunting to protect game populations (Reynolds & Tapper 1996; Cote & Sutherland 1997), but the assumption weakens when the carnivores neither depend on the property nor have evolved to use it. For example every wolf entering a farmed, white-tailed deer *Odocoileus virginianus* enclosure would probably compete against the owners, but only a minority of those wolves attack livestock on pastures in the same region (Wydeven *et al.* 2004; Chavez & Gese 2005, 2006). Among many large carnivore species, individuals differ in their tendencies to damage property. Usually a minority do so (Stander 1990; Sacks, Blejwas & Jaeger 1999; Angst 2001; Treves & Naughton-Treves 2005; Woodroffe & Frank 2005), but not always (Odden *et al.* 2002). Efforts to predict such conflicts with carnivores demand multivariate analyses of the characteristics of people, carnivores, property and wild resources (Bradley & Pletscher 2005; Packer *et al.* 2005; Wilson *et al.* 2006). Such complexity makes it unlikely that hunters could selectively target culprits, even with expert guidance. Indeed, age–sex classes of carnivores that damaged properties usually differed significantly from those of hunted animals (Faraizl & Stiver 1996; Linnell *et al.* 1999). Secondly, hunters have traditional hunting areas and habits which may not mesh well with control of problem carnivores (Heberlein 2000; Knight 2003). Those who prefer hunting in wilderness might displace carnivores to areas of higher human use, as seen in geese (Bechet *et al.* 2003; Cope, Vickery & Rowcliffe 2005). However, some hunters prefer hunting near private properties, which could improve the selective removal of problematic carnivores (Naughton-Treves 2002; Bunnefeld *et al.* 2006). Thirdly, hunters may injure their quarry, leaving carnivores more prone to turn to human foods because of their debility (Rabinowitz 1986; Marker *et al.* 2003). Even if the culprits are targeted selectively, property damage may increase if hunting disrupts carnivore social organization and promotes new individuals or new denser populations of different species of carnivores that, in turn, may have greater impacts on property (Gompper 2002; Robinson *et al.* 2008). Complex interactions within carnivore guilds compound the uncertainties about the effects of eliminating carnivores (Palomares *et al.* 1995; Crooks & Soule 1999; Smith, Peterson & Houston 2003). Thus, understanding carnivore and hunter behaviour is essential to the design and regulation of hunts to prevent property damage or competition over game.

Another assumption is that hunting can indirectly prevent damage by surviving carnivores, as when predation exerts an indirect effect by forcing prey to change behaviour to avoid attack (Lima 1998; Ripple & Beschta 2004). Carnivores at risk from hunters might avoid people and their ambits (references above). In the longer term, hunting might select against individual carnivores that have learned or inherited an attraction to people or their property (Jorgensen *et al.* 1978; Woodroffe & Frank 2005). The assumption that carnivores threatened by people will learn to avoid property is corroborated by the literature on non-lethal deterrence and guard animals (Smith *et al.* 2000a,b; Treves, Wallace & White 2009). In particular, when aversive stimuli are triggered in response to undesirable behaviour of wildlife (e.g. motion-activated electronic sirens and lights), one sees rapid learning that persists over time (Shivik, Treves & Callahan 2003; Shivik 2006). Likewise the defensive responses of livestock-guarding animals towards carnivores may act as aversive stimuli. Presumably, carnivores narrowly avoiding being shot, trapped or poisoned would experience aversion. Unfortunately, few explicit tests of the assumption of indirect effects have been reported in the literature.

There is clearly a complex interplay of direct and indirect effects of hunting with equivocal results in the scant scientific literature. It should come as no surprise that the outcomes of hunting undertaken to reduce property damages also vary. A review of US bounty systems found ‘no documented evidence indicating that bounty programmes temporarily or permanently reduce coyote *Canis latrans* abundance or subsequently reduce livestock depredations....’ (Bartel & Brunson 2003, p. 736; see also Berger 2006). Research on cougar hunting suggested that livestock attacks rose as a consequence of younger males that were more prone to attack livestock, replacing resident males taken by hunters (Weilgus, R. Unpublished data 2009; Robinson *et al.* 2008). Bear hunting illustrates the variable outcomes. Forbes *et al.* (1994) found reduced conflicts after a higher take of black bears around Fundy National Park, Canada, whereas research at three other sites found no such effect (Garshelis 1989; Obbard, Pond & Howe 1997; Kapp 2006). Analysing Japan’s annual hunter take of > 1000 Asiatic black bears *U. thibetanus*, Huygens *et al.* (2004) concluded damage costs were uncorrelated to hunter take, either in the same year or the year prior. By contrast, a study of European lynx hunting in Norway – where free-ranging sheep grazed without protection within predator habitat (Herfindal *et al.* 2005) – found hunter take of male lynx saved 13 lambs across a vast area in the first year – saving < 1 lamb per owner – and removal of female lynx saved two lambs over a smaller area. Little or no additional savings were detected after the first year. An observed correlation between estimates of the rate of lynx predation on sheep, the lynx population size, and hunter take of lynx was suggestive that hunters were reducing sheep losses (Herfindal *et al.* 2005). Yet, subsequent work indicated that these lynx distributed according to roe deer *Capreolus capreolus* availability not the distribution of much more abundant sheep (Odden *et al.* 2008). The complexity of predator–prey–livestock interactions hampers generalizations – slowing the process of translating research into policy.

HUNTING TO BUILD POLITICAL SUPPORT FOR CARNIVORE CONSERVATION (BUILD PUBLIC SUPPORT)

Regardless of conflict levels or carnivore population stability, hunting might generate broader political support or funding for carnivore conservation. Some experts predict that people with a legal right to hunt carnivores will feel more control or ownership over them (Linnell, Swenson & Andersen 2001; Hristienko & McDonald 2007; Heberlein 2008). This prediction is consistent with the theory that people’s perceptions of risk respond to individual control over environmental hazards (Starr 1969). A number of studies show correlations between various measures of tolerance for wildlife and variation in individual power, influence and coping strategies (reviewed in Naughton-Treves & Treves 2005; Treves *et al.* 2006). Similarly, people seem to accept dangerous or destructive animals more readily if they own or benefit from them (Mishra *et al.* 2003; Dekoninck 2005). Yet, tests of this idea were equivocal. A study of public attitudes toward brown bears found no difference among residents of a jurisdiction allowing bear hunting and those in a jurisdiction with bears but no bear hunting (Kaczensky, Blazic & Gossow 2004). Attitudinal research showed majority support in Sweden and Wisconsin, USA, for public hunting of grey wolves, provided the justifications included sustainability and protection of domestic animals or human safety (Ericsson *et al.* 2004; Heberlein & Ericsson 2005); A. Treves & K.A. Martin, unpublished data 2009). However, no explicit test of attitudes before and after carnivores became legal game have been reported in the literature.

Hunters may value carnivores most as game. Hence, they specifically may step forward as the champions of carnivore conservation (Mincher 2002; Heberlein 2008). Hunters often provide data useful to managers on demography, location and condition of game (Andersone & Ozolins 2000; Logan & Sweanor 2001; Sandstrom *et al.* 2009). Also hunters in North America and Europe have a long history of financial and political support for conservation of game and their habitats (Jackson 1996; Holsman 2000; Peterson 2004; Loveridge *et al.* 2007a,b). However, sceptics point out that most hunting revenues are compulsory, hence they reveal little about the willingness of hunters to conserve problematic wildlife. For example, an analysis of the role of US hunters as stewards of wildlife – written by a hunter – concluded that ‘... hunters often hold attitudes and engage in behaviours that are not supportive of broad-based, ecological objectives...’ (abstract) and ‘...the behaviours of hunter groups and individuals are often counter to desired needs of ecosystem stewardship.’ (Holsman 2000, p. 813). However, hunters in Wisconsin and the Northern Rocky Mountains, USA, studied between 2001 and 2007 were not ready to champion wolf or grizzly bear conservation, as assessed by independent third-party criteria (A. Treves & K.A. Martin, unpublished data 2009). Therefore, governments and wildlife agencies cannot assume hunters will support maintenance of ecologically functional carnivore populations simply because they have in the past for other game (Holsman 2000).

Alternatively, hunters may feel less inclined to kill carnivores outside the hunting season because they value them as game. Reducing illegal killing of carnivores is important given that humans remain the major causes of large-carnivore mortality worldwide. However, long-term studies of lynx hunting in Scandinavia and wolf hunting in North America found little or no association between higher legal take and illegal killing (Andren *et al.* 2006; Adams *et al.* 2008; Person & Russell 2008).

Gaps are evident in our understanding of attitudes to hunting carnivores among the broader public and hunters specifically. Attitudes to carnivores and to hunting expose different meanings of coexistence to different peoples. Those favouring hunting may view control or dominance of the carnivores as essential to coexistence. Those opposing hunting may view coexistence as a more equitable or peaceful proposition and favour non-lethal methods. Even when attitudinal data are available, finding a balance between such opposing views will be a perennial challenge (Clark & Primm 1996; Campbell & Mackay 2009; Sandstrom *et al.* 2009).

Conclusions

When one focuses on three common goals of public hunting of carnivores to maintain stable populations at target levels, reduce property loss and build broad public support for carnivore conservation, one finds critical gaps in scientific knowledge. In brief, sustainable hunting to maintain stable populations is well understood in theory but stochastic events, life-history patterns, social systems of carnivores, and complex behavioural changes of hunters and the carnivores they stalk, can be expected to thwart our predictions and demand long-term, landscape-level, costly monitoring. In practice, uncertainties could result in unsustainable off-take. Secondly, the direct impact of hunting on conflicts with carnivores over game and property damage is unclear and even doubtful given the inability or unwillingness of hunters to remove specific individuals selectively. However, hunters may indirectly deter carnivores from people and their property. Finally, we still cannot be certain if hunters will show stewardship of carnivores once they are designated as legal game. Scant evidence warrants caution. Indeed, any conclusions would have limited value as generalities until more experimental studies of hunter-carnivore systems are conducted. Scientists must disentangle opposed hypotheses if they wish to inform policy (Table 1). This will require interdisciplinary research, some experimentation and careful monitoring at local and regional scales.

Sensitive monitoring at many levels and careful design of hunting seasons may help to achieve politically acceptable hunting that conserves large carnivores and reduces property damage. Five steps should be taken in logical sequence before and after a hunting strategy is implemented: (i) study hunter behaviour and measure attitudes among arrays of stakeholders, (ii) promote hunter participation and rules for hunting that are consistent with the explicit goals of the hunt, (iii) raise non-hunter confidence by transparent dissemination of the outcomes of a hunt, (iv) analyse carnivore behaviour and population ecology, both inside and outside the hunting zones, and (v) measure property damage and wild prey abundances before and after the hunt.

Policy-makers may achieve support for policy if they mesh utilitarian and preservationist values held by the general public and come to grips with scientific uncertainties about the effectiveness and ecological consequences of carnivore hunts. Unfortunately, policy-makers may not be willing to wait for balanced, interdisciplinary, long-term research in the face of vociferous interest groups. Judging from the many arguments put forward by proponents and opponents, carnivore-hunting policy for a particular jurisdiction will most probably reflect the managers' and decision-makers' own experiences, individual attitudes and political pressures, more than the results of scientific studies. Political clashes are likely to fuel controversy over carnivore conservation for years to come.

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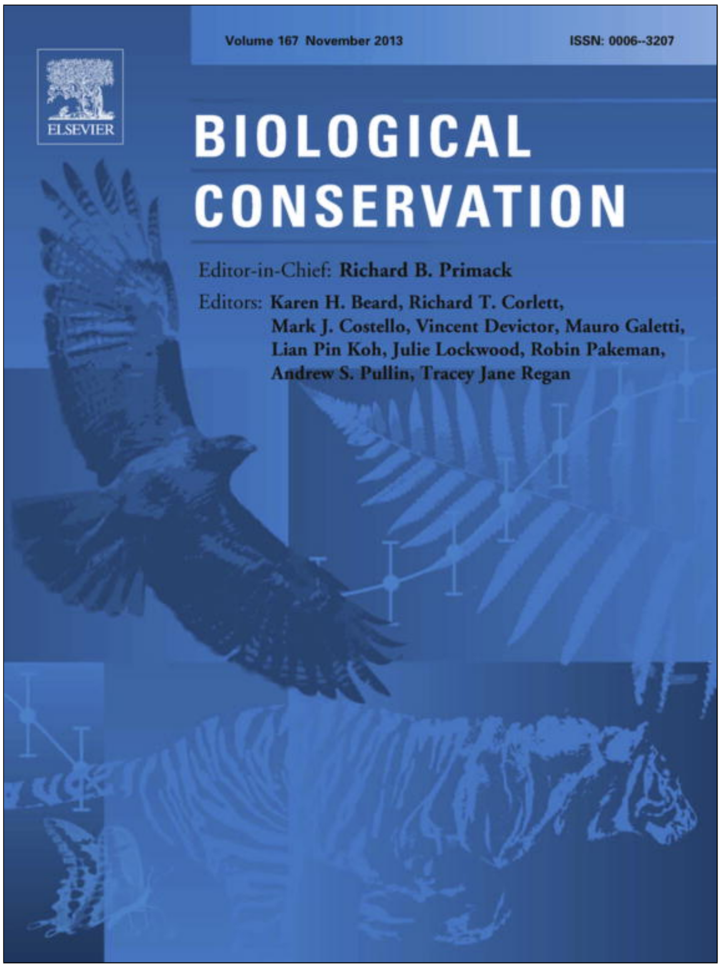
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Effects of male trophy hunting on female carnivore population growth and persistence

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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 acrtos*) 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 polygnous 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.

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

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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 Sweanor, 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 depensatory dynamics were later suggested for cougars (Logan and Sweanor, 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 depensatory (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, depensatory 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 km^2, 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 km^2 (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 km^2. 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 (*Psuedosuga 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 Northeast Washington State and includes a mix of federal, state, and privately owned land and covers 735 km^2. 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 tacking 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 (Akcakaya, 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)		
	n	Hunting	Natural/other	*n*	Hunting	Natural/other
Kitten[a]	23	0.00 ± 0.00	0.69 ± 0.18	19	0.00 ± 0.00	0.42 ± 0.17
Juvenile[b]	18	0.31 ± 0.12	0.07 ± 0.00	13	0.23 ± 0.21	0.15 ± 0.13
F Adult[c]	19	0.22 ± 0.07	0.12 ± 0.06	12	0.04 ± 0.04	0.09 ± 0.06

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

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

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, 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 depensatory 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 depensatory 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 (depensatory 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 depensatory 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 depensatory 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.

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