Wildlife Society Bulletin; DOI: 10.1002/wsb.299

In My Opinion

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

RICHARD A. BEAUSOLEIL,[1] *Washington Department of Fish and Wildlife, 3515 State Highway 97A, Wenatchee, WA 98801, USA*
GARY M. KOEHLER, *Washington Department of Fish and Wildlife, 2218 Stephanie Brooke, Wenatchee, WA 98801, USA*
BENJAMIN T. MALETZKE, *Washington Department of Fish and Wildlife, P.O. Box 522, Pullman, WA 99163, USA*
BRIAN N. KERTSON, *Washington Department of Fish and Wildlife, 1775 12th Ave NW, Suite 201, Issaquah, WA 98027, USA*
ROBERT B. WIELGUS, *Large Carnivore Conservation Lab, Washington State University, Pullman, WA 99163, USA*

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.

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

Received: 30 July 2012; Accepted: 6 February 2013

[1] *E-mail: richard.beausoleil@dfw.wa.gov*

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

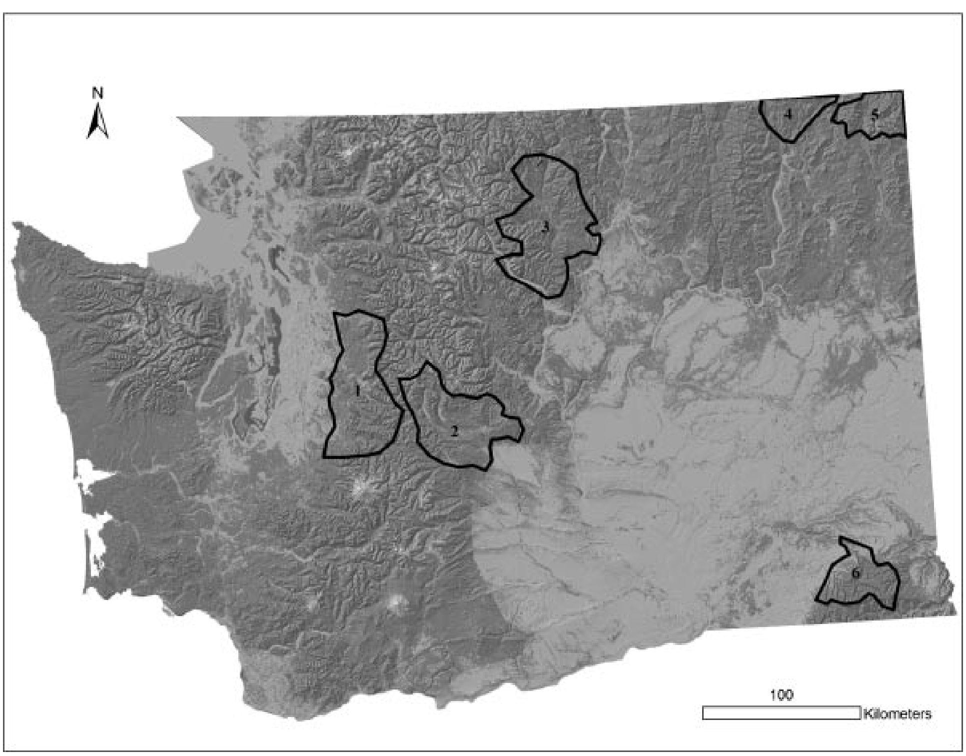

Figure 1. Six cougar research areas in Washington, USA, 2001–2012: (1) western WA; (2) central WA; (3) north-central WA; (4 and 5) northeast WA; (6) southeast WA.

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 where 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

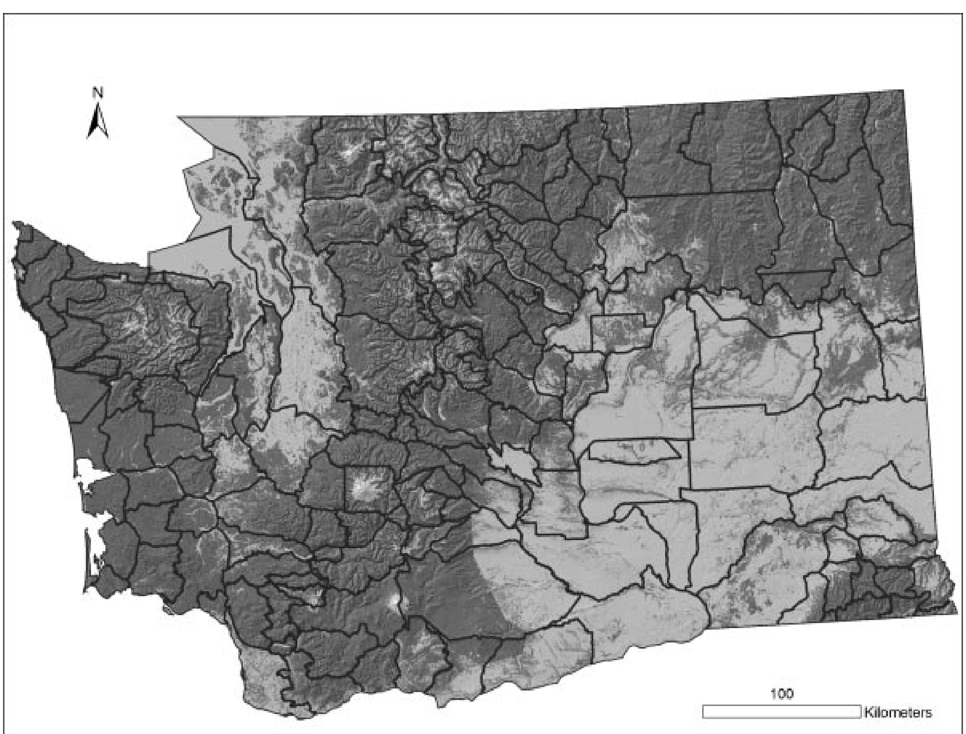

Figure 2. Distribution of cougar habitat (shaded dark) and current game-management units (outlined in black) in Washington, USA, Washington Department of Fish and Wildlife, 2012.

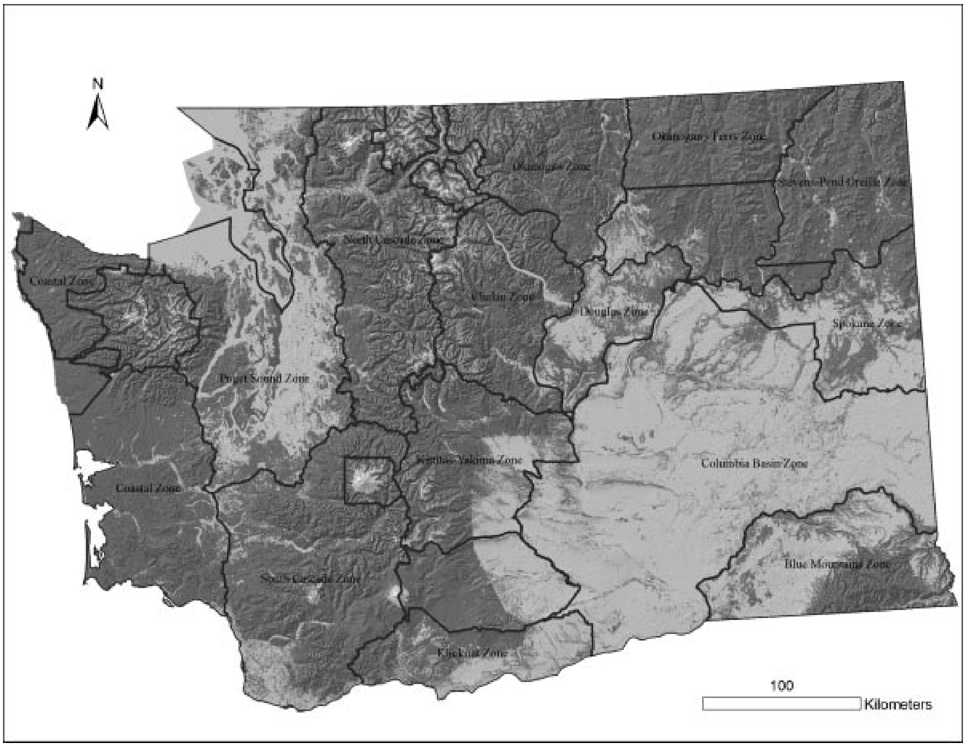

Figure 3. 2011 cougar management zones in Washington, USA, Washington Department of Fish and Wildlife, 2012.

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

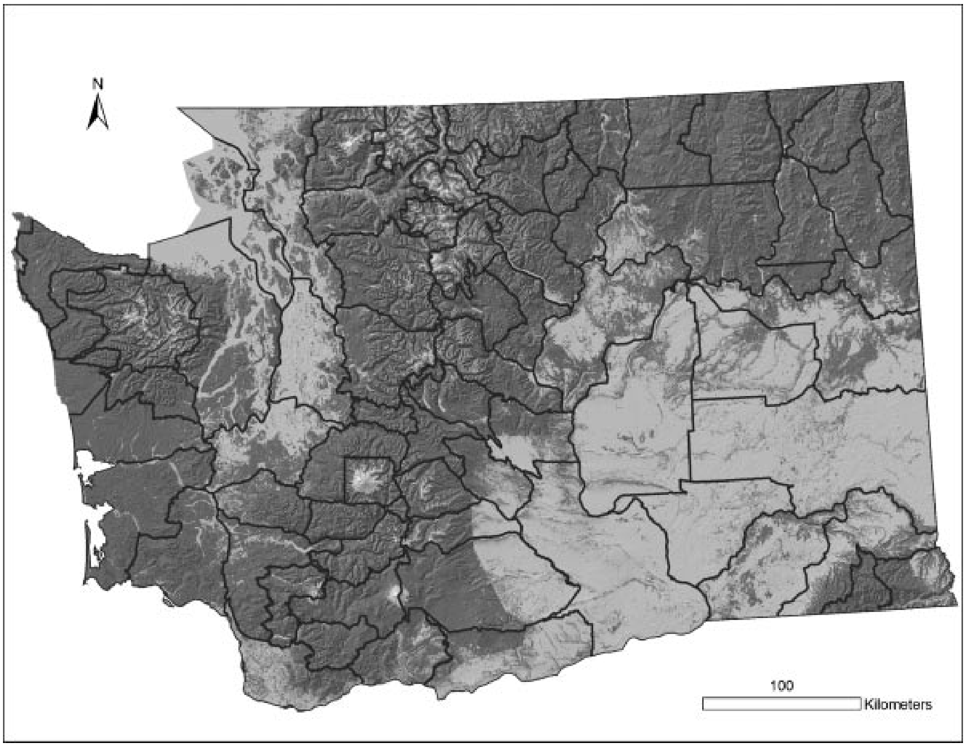

Figure 4. Proposed cougar management zones for Washington, USA, 2012.

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.

ACKNOWLEDGMENTS

We thank M. G. Hornocker, H. S. Robinson, and H. S. Cooley for comments that helped improve the initial manuscript. S. Haskell, K. Knopff, and an anonymous reviewer provided a constructive critique. We would also like to thank the highly experienced hound handlers involved in making our projects successful; they include D. Clark, R. Culver, K. Lester, D. Likens, S. Reynaud, R. Schultz, B. Smith, C. Smith, and M. White.

LITERATURE CITED

Beausoleil, R. A., D. Dawn, D. A. Martorello, and C. P. Morgan. 2008. Cougar management protocols: a survey of wildlife management agencies in North America. Pages 205–241 *in* D. E. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the Ninth Mountain Lion Workshop. Idaho Department of Fish and Game, Sun Valley, Idaho, USA.

Beausoleil, R. A., and D. A. Martorello. 2008. Washington mountain lion status report. Pages 18–22 *in* D. E. Toweill, S. Nadeau, and D. Smith, editors. Proceedings of the Ninth Mountain Lion workshop. Idaho Department of Fish and Game, Sun Valley, Idaho, USA.

Beecham, J. J., and J. Rohlman. 1994. A shadow in the forest: Idaho's black bear. University of Idaho Press, Moscow, USA.

Burdett, C. L., K. R. Crooks, D. M. Theobald, K. R. Wilson, E. E. Boydston, L. M. Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:4.

Caro, T. M., C. R. Young, A. E. Cauldwell, and D. D. E. Brown. 2009. Animal breeding systems and big game hunting: models and application. Biological Conservation 142:909–929.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell Science, Malden, Massachusetts, USA.

Cooley, H. S., H. S. Robinson, R. B. Wielgus, and C. S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. Journal of Wildlife Management 72:99–106.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, and B. T. Maletzke. 2009*a*. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation 12:321–328.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009*b*. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. First edition. WildFutures, Bainbridge Island, Washington, USA.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Hornocker, M. G. 1969. Winter territoriality in mountain lions. Journal of Wildlife Management 33:457–464.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. Wildlife Monographs 21.

Hornocker, M., and S. Negri. editors, 2010. Cougar: ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Jenks, J. A. 2011. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, Utah, USA.

Katnik, D. D. 2002. Predation and habitat ecology of mountain lions (*Puma concolor*) in the southern Selkirk mountains. Dissertation, Washington State University, Pullman, Washington, USA.

Kertson, B. N. 2005. Political and socio-economic influences on cougar management in Washington State: post Initiative. Pages 92–103 *in* R. A. Beausoleil, and D. A. Martorello, editors. Proceedings of the Eighth Mountain Lion workshop. Washington Department of Fish and Wildlife, Olympia, Washington, USA.

Kertson, B. N. 2010. Cougar ecology, behavior, and interactions with people in a wildland–urban environment in western Washington. Dissertation, University of Washington, Seattle, USA.

Kertson, B. N., R. D. Spencer, and C. E. Grue. 2011*a*. Cougar prey use in a wildland–urban environment in western Washington. Northwestern Naturalist 92:175–185.

Kertson, B. N., R. D. Spencer, and C. E. Grue. 2013. Demographic influences on cougar residential use and interactions with people in western Washington. Journal of Mammalogy 94:269–281.

Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011*b*. Cougar use and movements in the wildland–urban landscape of western Washington. Ecological Applications 21:2866–2881.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

LANDFIRE. 2007. Existing Vegetation Type layer (EVT). U.S. Department of Interior Geological Survey. http://www.landfire.gov/index.php. Accessed 02 Dec 2011.

Laundré, J. W., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. Animal Conservation 6:159–170.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D. C., USA.

Logan, K. A., and L. L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105–117 *in* M. G. Hornocker, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Illinois, USA.

Maletzke, B. T. 2010. Effects of anthropogenic disturbance on landscape ecology of cougars. Dissertation, Washington State University, Pullman, USA.

Martorello, D. A., and R. A. Beausoleil. 2003. Characteristics of cougar harvest with and without the use of dogs. Pages 129–135 *in* S. A. Becker, D. D. Bjornlie, F. G. Lindsay, and D. S. Moody, editors. Proceedings of the Seventh Mountain Lion workshop. Wyoming Game and Fish Department, Lander, Wyoming, USA.

Martorello, D. M., R. A. Beausoleil, and R. D. Spencer. 2006. Cougar status and trend report. Pages 170–172 *in* 2006 Game status and trend report. Washington Department of Fish and Wildlife, Wildlife Program, Olympia, Washington, USA.

Mattson, D. J., and S. G. Clark. 2010. People, politics, and cougar management. Pages 206–220 *in* M. G. Hornocker, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Illinois, USA.

Merrill, J. A., E. G. Cooch, and P. D. Curtis. 2006. Managing an overabundant deer population by sterilization: effects of immigration, stochasticity and the capture process. Journal of Wildlife Management 70:268–277.

Mills, L. S. 2013. Conservation of wildlife populations: demography, genetics, and management. Second edition. John Wiley and Sons, Malden, Massachusetts, USA.

Morrison, D. E. 2010. Effects of trophy hunting on female cougar population growth and persistence. Thesis, Washington State University, Pullman, USA.

Packer, C., M. Kosmal, H. S. Cooley, H. Brink, L. Pintea, D. Garshelis, G. Purchase, M. Strauss, A. Swanson, G. Balme, L. Hunter, and K. Nowell. 2009. Sport hunting, predator control and conservation of large carnivores. PLoS ONE 4:1–8.

Peek, J., B. Dale, H. Hristienko, L. Kantar, K. A. Loyd, S. Mahoney, C. Miller, D. Murray, L. Olver, and C. Soulliere. 2012. Management of large mammalian carnivores in North America. Technical Review 12-1. The Wildlife Society, Bethesda, Maryland, USA.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543.

Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59–75 *in* M. G. Hornocker, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, Illinois, USA.

Robinson, H. S., and R. M. DeSimone. 2011. The Garnet Range mountain lion study: characteristics of a hunted population in West-central Montana. Final report, Montana Department of Fish, Wildlife, and Parks, Wildlife Bureau, Helena, Montana, USA.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80:556–568.

Ross, P. I., M. G. Jalkotzy, and J. R. Gunson. 1996. The quota system of cougar harvest management in Alberta. Wildlife Society Bulletin 24:490–494.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation level in Utah; implications for demographic structure, population recovery and metapopulation dynamics. Journal of Wildlife Management 70:1588–1600.

Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois, USA.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350–1356.

Turgeon, K., and D. L. Kramer. 2012. Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity. Journal of Animal Ecology 81:1161–1170.

Van Ballenberghe, V. 2011. Intensive management-or mismanagement? Exploring Alaska's predator control programs. The Wildlife Professional (Winter) 74–77.

Washington Department of Fish and Wildlife [WDFW]. 2008. 2009–2015 Game management plan. Washington Department of Fish and Wildlife, Wildlife Program, Olympia, Washington, USA.

Washington Department of Fish and Wildlife [WDFW]. 2011. 2011 Game status and trend report. Washington Department of Fish and Wildlife, Wildlife Program, Olympia, Washington, USA.

Way, J. G., and J. T. Bruskotter. 2012. Additional considerations for gray wolf management after their removal from endangered species act protections. Journal of Wildlife Management 76:457–461.

White, K. R., G. M. Koehler, B. T. Maletzke, and R. B. Wielgus. 2011. Differential prey use by male and female cougars in Washington. Journal of Wildlife Management 75:1115–1120.

Wielgus, R. B., and F. L. Bunnell. 1994. Dynamics of a small hunted brown bear population in southwestern Alberta, Canada. Biological Conservation 67:161–166.

Associate Editor: Haskell.